Southern Newfoundland Waters Under Changing Ocean Conditions: Diets and Spatial Distributions of Emerging and Re-Emerging Gadoids Within NAFO Subdivision 3Ps

by

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Abstract

Quantifying species interactions and spatial dynamics increases understanding of ecosystem function in marine environments affected by climate change. The region containing Newfoundland's warmest, most spatially variable sea temperatures historically supported large haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) fisheries. Recently, spring survey catches contained pollock (*Pollachius virens*) and silver hake (*Merluccius bilinearis*), gadoids typically more abundant farther south. Recent increases in spring bottom temperatures may lead to the establishment of these 'southern' species, with implications for resident species. Analyses of diet and spatial data of four gadoids relative to temperature increases over time were used to better understand a transitioning ecosystem. Atlantic cod had the most varied diet of the four species, while haddock consistently consumed mainly benthic prey. Pollock and silver hake were more piscivorous, with the level of piscivory increasing with body size. Pollock exhibited no significant spatial shifts, while silver hake shifted northward, increased in abundance and biomass, and expanded its range within the region. Atlantic cod and haddock were caught more frequently in cooler waters, and the mean depth at which cod was caught decreased over time. The gadoids had distinct depth distributions, potentially contributing to low degrees of diet overlap.

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General Introduction

The global effects of climate change are forecast to be far reaching. Impacts have been and will be seen in both aquatic and terrestrial systems, and the stresses on marine systems are expected to be intense (Doney et al. 2012, IPCC 2014). This is partly because the marine environment experiences climate velocities (spatial-temporal shifts of equal temperature regions) that are heterogeneous across ocean basins and up to seven times higher than within terrestrial systems (Walther et al. 2002, Burrows et al. 2011, Pinsky et al. 2013). In addition to global warming fuelled by anthropogenic activities, the planet is currently in a warm period of multi-decadal global climatic cycling (NOAA 2012). This cycling is synergistic with the effects of human-induced climate change and can lead to enhanced warming of marine and terrestrial environments.

In marine systems, a number of potential other abiotic effects have been predicted. Some examples of these predictions are: changes in salinity from altered precipitation patterns and melting permafrost, sea and land ice, with decreased sea ice thickness and cover (Frank et al. 1990, Doney et al. 2012); increased run-off from land due to more frequent and prolonged precipitation, leading to possible eutrophication from augmented nutrient, sediment, and carbon loadings in coastal areas (Wrona et al. 2006); and changes in light intensity penetration through the water column due to particulates, plankton, algal blooms in the water, and changes in ice cover (Jonsson and Jonsson 2009). Furthermore, an increase in the frequency, duration, and intensity of extreme weather events has been predicted (Mika 2013), and based on current CO_2 concentrations it has been forecasted that ocean pH will decrease as more carbon dioxide is dissolved into the water leading to more acidic conditions (Crawfurd et al. 2011, Doney et al. 2012). Finally, the most frequently discussed consequences of climate change are increases in

mean temperature and temperature variability, conditions that are consistently linked to the patterns and dynamics of marine species' distributions (Tittensor et al. 2010). In this study, my focus was on the diets and effects of increases in bottom water temperatures on spatial distributions of gadoid species.

Some of the abiotic factors listed above can impact biological interactions such as intra- and inter-specific competition, size-specific predation rates, and growth rates which can in turn affect predator-prey interactions in marine systems (Frank et al. 1988, Best et al. 2007, Dulvy et al. 2008). Oceanographic changes also influence biogeography, dispersal, migration, survival, and species abundance and richness (Frank et al. 1990, Murawski 1993, McCarty 2001, Perry et al. 2005, Rose 2005a, Dulvy et al. 2008, Cheung et al. 2009, Nye et al. 2009, Tittensor et al. 2010, Last et al. 2011). Given this background, my research specifically examined gadoid species' trophic interactions and species distributions over time.

Many recent studies support the generality that as seawater temperature increases, the majority of mobile marine species shift their distributions poleward toward more thermally optimal habitat (e.g. Frank et al. 1990, Murawski 1993, Pörtner 2002, Rahel 2002, Walther et al. 2002, Drinkwater 2005, Perry et al. 2005, Barange and Perry 2009, Chen et al. 2011, Last et al. 2011, Perry 2011, Hare et al. 2012, Nye et al. 2014). However, some studies have shown that some species change their depth distributions to occupy more favourable thermal conditions in lieu of a poleward shift (Dulvy et al. 2008, Pinsky et al. 2013). Even if a species' geographic range doesn't shift, abundances may increase at the poleward extent and decrease at the equatorial extent of their distribution (Rijnsdorp et al. 2009, Last et al. 2011). Marine organisms closely track changing thermal conditions (Nye et al. 2011), even more so than terrestrial

organisms because marine ectotherms inhabit a geographical range more closely conforming to their thermal tolerance limits (Sunday et al. 2012).

In practice, there has been notable heterogeneity in distributional shifts in response to changing ocean conditions. For example, Dulvy et al. (2008) quantified shifts at the species level and found that distributional shifts were influenced by both abundance and whether that species was a thermal generalist. In contrast, Pinsky et al. (2013) found shifts in distribution at the ecosystem level were largely explained by the rate and direction that isotherms changed within an ecosystem. Given these results, distributional shifts and associated changes in spatial overlap and trophic interactions may be expected in areas identified as biogeographic boundaries. In the Northwest Atlantic, such an area exists in the vicinity of southern Newfoundland at 47°N near Cape Race, separating fish assemblages associated with the Nova Scotian biogeographical province from the Labrador/Arctic biogeographical province (Pinhorn and Haliday 1997, Mahon et al. 1998, Spalding et al. 2007, Wilkinson et al. 2009).

The warmest and most spatially variable temperatures in Newfoundland waters are found in Northwest Atlantic Fisheries Organization (NAFO) Statistical Subdivision 3Ps (Figure 1.1a, Figure 1.1b, Colbourne et al. 2013, Morgan et al. 2013). It borders the south coast of Newfoundland and includes Burgeo Bank, St. Pierre Bank, and most of Green Bank. It is bordered by Hermitage and Laurentian Channels and also contains Halibut Channel. This region contains both shallow shelf habitat, which in spring is covered in cold (< 1°C) water derived from the southward flowing Labrador Current, and a shelf slope bathed by comparatively warmer (4-7°C), northward flowing Atlantic slope water (Pershing et al. 2001). This not only provides 3Ps with complex temperature gradients across the entire region, but when two currents

converge on a shelf slope, upwelling of nutrient-rich water (Stenseth et al. 2002) leads to high biomass and production (Demarcq 2009).

In the context of changing regional ocean conditions, Belkin (2009) found that sea surface temperature within the Newfoundland and Labrador shelf large marine ecosystem had a 1.04 degree Celsius net increase from 1982 to 2006, which was the 5th largest change in a ranking of 63 systems. In 3Ps, similar trends have been observed in bottom water temperatures. Long-term monitoring by Fisheries and Oceans Canada (DFO) has revealed recent, anomalous increases in bottom temperatures with reductions in thermal habitat areas below 0°C and increases in habitats above 2°C (Colbourne et al. 2013). More specifically, there has been an average 0.03°C annual increase in bottom temperature since 1993 (Figure 1.2c), with especially warm temperatures in 2011 and 2012 (Colbourne et al. 2014, DFO 2014a, DFO 2015a). In the spring of 2012, bottom temperatures were above normal by about 1°C (Figure 1.1b), which was a moderate decrease from conditions in the spring of 2011. These types of thermal shifts have been associated with distributional shifts, particularly increases in abundance of more 'southern' species at the northern extents of their ranges. This has been observed in nearby Northwest Atlantic ecosystems (Nye et al. 2009, Nye et al. 2013) and may be one of many factors, another example being fisheries exploitation, which can lead to reductions or local extinctions of northern and less cosmopolitan resident species (Hughes 2000, Stortini et al. 2015).

Such warming, as observed in 3Ps (Figure 1.1b, Figure 1.2c), may lead to the establishment and persistence of species that thrive in warmer temperatures, with potential implications for locally resident fish species, specifically Atlantic cod (*Gadus morhua*). This species supported commercial fisheries for centuries, was briefly under a moratorium in the mid-1990s, and is currently in the 'cautious' zone under the DFO Precautionary Approach (DFO

2015a). Under favourable conditions, some species tend to emerge in new areas more quickly than resident species retreat, which can lead to a temporal mismatch in spatial shifts and the possibility of temporary changes in species assemblages and interactions (Cushing 1974, Walther et al. 2002, Schweiger et al. 2008, Kempf et al. 2010). The temporal mismatch hypothesis describes potential shifts of mobile predator and prey distributions, and is a possible explanation for changes in not only competitive, but also predator-prey and trophic interactions (Cushing 1974).

During the Centre for Fisheries Ecosystems Research (CFER) offshore ecosystem surveys aboard the Research Vessel *Celtic Explorer* in spring 2012-2014, investigations of acoustic fish signals in Subdivision 3Ps yielded samples of fish species that are typically more abundant farther south. Among these species were haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), and silver hake (*Merluccius bilinearis*). Although some of these species have appeared in the past or have inhabited 3Ps for a number of years, these initial CFER survey results suggested that this new information or an increased understanding of the spatial distributions and potential interactions among gadoid species would provide insight for fisheries management.

Atlantic cod is a local resident and once supported a large fishery in 3Ps. In the 1960s and early 1970s, Canadian and non-Canadian fleets landed between 45,000 and 85,000 tonnes per year. After catches decreased to a record low 15,000 tonnes in 1993, a three-year moratorium was initiated. Between 1997 and 2008, the total allowable catch (TAC) varied between 10,000 and 30,000 tons. From 2009 to 2014, the TAC was set at 11,500 tonnes, although reported landings have been below this number every year, and since 2011 only about half of the TAC has been landed (DFO 2015a).

Historically, cod was the dominant piscivore in 3Ps by biomass, but in recent years, its dominance in scientific surveys appears to be in decline as silver hake and pollock biomass increase (DFO 2014a). In 2014 spring surveys (Figure 1.2a, Figure 1.2b), silver hake for the first time replaced Atlantic cod as the dominant piscivore species by biomass (DFO 2015a) and this species has become much more prevalent in the adjacent northern Gulf of St. Lawrence (Archambault et al. 2014) and high abundances have returned to the Scotian Shelf (DFO 2013, DFO 2015b), where its geographic distribution is positively related to stock size (Fisher and Frank 2004) and its ability to inhabit a wider temperature range leave it among the most resilient to projected climate warming (Stortini et al. 2015). At present, silver hake stock assessments on the adjacent Scotian Shelf region (NAFO Divisions 4VWX) do not include information from the Newfoundland region (Stone et al. 2013, DFO 2015b), although whether these stocks are distinct has not yet been studied. Increases in abundance of piscivorous predators like silver hake have the potential to impact the assemblages of not only their finfish prey, including the early life stages of gadoids (Temming et al. 2007), but also predators that are competing for the same resources (Helser et al. 1995); however, the trophic role of silver hake in Newfoundland waters remains unquantified.

Given their historic spatial distributions predominantly over the Scotian Shelf, Gulf of Maine, and Georges Bank, pollock and silver hake are considered emerging gadoids at the northern edges of their geographic distributions in Newfoundland waters (McKenzie and Scott 1956, Helser et al. 1995, Pinhorn and Haliday 1997, Mahon et al. 1998). For example, the Canadian stock assessment of silver hake is restricted to NAFO 4VWX, south of Newfoundland waters and the Gulf of St. Lawrence (DFO 2013). In southern regions, silver hake has been found to closely track ocean conditions and temperatures, such that in US waters Nye et al.

(2011) suggested the distribution and abundance of this commercially important species ($7 million landed value annually) could be forecast based on ocean conditions. Such spatial dynamics have implications for gadoid stock assessments, fisheries productivity, and fisheries opportunities (Link et al. 2011, Helser and Alade 2012), and as a result of large catches of silver hake in research surveys since 2011, local fish harvesters have become interested in developing a potential fishery for this species in 3Ps.

Haddock is a formerly abundant resident species characterized by highly variable recruitment (Myers 1991) that was historically overexploited in 3Ps, with a peak catch of 58,000 tonnes in 1955, but has not supported large catches in this region since the 1960s (Templeman and Bishop 1979). Haddock has been under a direct fishery moratorium in subdivision 3Ps since 1993, as there has been no evidence of stock size increase, but the 3Ps stock has only been fully assessed once since 2001 (DFO 2014b).

Since its inception, CFER has had a goal to understand not only commercially significant fish stocks, but also the fish and invertebrate populations surrounding Newfoundland and Labrador that are not targeted by fisheries. Implementing an ecosystem-based approach to fisheries resource management is important. Single-species approaches have limitations (Link 2002a) and many economically valuable finfish species are strongly interconnected with other fish and invertebrate species in the trophic food web (Savenkoff et al. 2001, Heymans and Pitcher 2004, Pitcher and Forrest 2004, Francis et al. 2007, Nye et al. 2013). As fisheries management strategies and stock assessments evolve from a single-stock approach to an ecosystem-based approach, it will be crucial that species interactions are considered in the context of management (Link and Garrison 2002). Trophic interaction and food web data can be

used to look at the ecosystem on a broader scale (Pinkas et al. 1971, Link and Almeida 2000, Hornborg et al. 2013).

The purpose of my research was to gain a better understanding of the impacts of local and global climate change and climate cycles on gadoid fish assemblages in southern Newfoundland waters by quantifying their diets and spatial distributions in 3Ps. This region has historically been a habitat range endpoint for many species in the family gadidae (Pinhorn and Halliday 1997). Therefore, I assessed the potential for intaguild predation, competition for prey and competition for space between Atlantic cod and emerging and re-emerging 'southern' gadoids partly as a result of changing abiotic conditions. Specifically, I compared diet and spatial distribution data between Atlantic cod, haddock, pollock, and silver hake. For diet especially, the goal was to gain more insight into potential competition and predation in this area, and what these interactions suggest for resident Atlantic cod. For the spatial aspect, increases in bottom temperatures would increase thermally appropriate habitat for 'southern' species that have northern range limits in this ecosystem. Therefore, I looked at directional shifts, changes in range extent, and changes in abundance of four gadoid species, and biomass of three non-cod gadoid species.

The broader scope of the project was to look at possible changes in species assemblages and interactions as a function of changing ocean conditions, as temperatures have warmed in recent decades. An increase in understanding contributes to the development of appropriate and effective management strategies critical to the maintenance of ecosystem function, including the provision of fisheries yields (DFO 2015a). This study provided new information about these species, information that was presented within the Atlantic cod stock assessment (DFO 2015a), especially with regards to diets and the magnitude of silver hake increase in 3Ps. This species is

now competing with Atlantic cod to be the most dominant gadoid piscivore, by biomass in this region.

For the reasons mentioned above, the diet composition and spatial distribution results my research provide, especially for growing numbers of silver hake, are important for fisheries management, and should be considered in future stock assessments. Further, the closest silver hake assessment is for the Scotian Shelf (DFO 2013), and in that assessment, no data from Newfoundland waters are used although there are large abundances of silver hake in this region that may interact with, or be derived from, the Scotian Shelf stock. This study found that there was a significant abundance of this species in 3Ps, and as such should be monitored and assessed in more detail than what is accomplished by the current multi-species surveys conducted by DFO. For example, surveying at other times of the year would help determine whether this stock is distinct from the 4VWX stock, or if data from this region should be part of assessments in adjacent areas.

Chapter 1. Comparative diet analyses of four co-occurring gadoid species in southern Newfoundland waters

1.1 Abstract

Increasing bottom water temperatures as a result of climate change and global climate cycles may influence the biogeography of marine fishes. Such changing ocean conditions can lead to poleward distributional shifts that may result in novel competitive and predatory interactions between local species and those moving poleward with warming temperatures. I undertook stomach content analyses of more than 2900 samples to understand the functional overlap between resident Atlantic cod (*Gadus morhua*) and other gadoid species that are increasing in abundance at the northern edges of their ranges. Northwest Atlantic Fisheries Organization (NAFO) Subdivision 3Ps is a faunal and thermal transition zone that in spring contains complex temperature gradients spanning cold, shallow shelf habitats to warmer shelf slopes and channels. Data collected primarily on the edges and slopes of the continental shelf on acoustic trawl surveys in the spring in 3Ps yielded samples of Atlantic cod as well as haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), and silver hake (*Merluccius bilinearis*). These three gadoids are typically more abundant farther south, with northern range limits in this region. Analyses revealed that cod had the most varied and generalist diet, while haddock had the least varied and most benthivorous diet, and piscivory increased with increasing size for pollock and silver hake. Quantitative analyses suggested that competition and intraguild predation were not occurring among the four species in the spring.

1.2 Introduction

The global impacts of climate change are predicted to be far reaching with intense stresses on the marine environment (Doney et al. 2012). Abiotic changes can influence distributional shifts leading to novel spatial overlap and changes in predator and prey communities (Cushing 1974, Kempf et al. 2010). Furthermore, altered species interactions are expected to multiply the effects of climate change on species distributions (Zarnetske et al. 2012). Together, these influences impact species interactions such as intra- and interspecific competition, growth rates, and size-specific predation rates, which can in turn affect predator-prey interactions in marine systems (Frank et al. 1988, Best et al. 2007). It is imperative that the rates and spatial extent of predation are quantified, as these provide information on the structure and the degree of connectedness of an ecosystem and potential competition (Cook and Bundy 2010). In dynamic marine ecosystems, it is important to monitor the diets of species that are emerging (those with novel increases in abundances) and re-emerging (those that have returned following previous declines) in order to better predict changes in prey abundances and trophic interactions (Garrison and Link 2000a, Garrison and Link 2000b, Worm and Myers 2003, Link et al. 2008, Cook and Bundy 2012).

As temperatures change, organisms that are able, tend to shift distributions to stay within the bounds of thermally optimal habitat (Hughes 2000, Rahel 2002). In the northern hemisphere, warmer ocean conditions often lead to increased prevalence of species along the northern extents of their geographic ranges, restriction of the ranges of resident species, and new instances of overlap and trophic interaction between local species and those that are increasing in the ecosystem (Barry et al. 1995, Kempf et al. 2010, Windle et al. 2012). Increases in bottom temperature may promote the establishment and persistence of species that thrive in warmer

temperatures (see also Chapter 2). Such changes have also been observed in other Northwest Atlantic regions (Nye et al. 2009, Nye et al. 2011, Nye et al. 2013) and can have implications for resident species and the potential to alter trophic interactions (Hughes 2000).

Stomach content analyses can be used to investigate trophic interactions and consumption on relatively narrow temporal, spatial, or ontogenetic scales. This method allows for a quantitative measure of diet, and provides a high-resolution snapshot of what predators are eating at a specific moment in time (Atwell et al. 1998, Baker et al. 2014), compared to stable isotopes, fatty acids, and other methods used for trophic analyses. Quantitative stomach content analyses also underlie the construction of food web models that describe species interactions and trophic structure (Christensen 1995, Albouy et al. 2011).

Findings from this study can be compared to diet information reported from adjacent stocks. Food habits data were available for this region for Atlantic cod (*Gadus morhua*) (Link et al. 2009, K. Krumsick unpublished data), but the same information was not available for the other species of interest: haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), and pollock (*Pollachius virens*). Much of the knowledge of what the other species of interest consumed was focused on the northeast US continental shelf and the Scotian Shelf (e. g. Durbin et al. 1983, Bowman 1984, Waldron 1992, Helser et al. 1995, Garrison and Link 2000a, Garrison and Link 2000b, Link and Almeida 2000, Laurinolli et al. 2004, Cook and Bundy 2010, Cook and Bundy 2012). Currently, there is a knowledge gap with regard to what non-cod gadoids eat in this area and if they are preying upon early life history stages of cod. To investigate food habits and intraguild predation, I quantified which prey species were most abundant in each predator's diet.

Recent changes in spatial distributions and abundances of gadoids such as haddock, silver hake, and pollock suggest the potential for restructuring of trophic interactions in this region. Therefore, I quantified both potential species interactions and single species diet dynamics using stomach content analyses. My primary objective was to quantify single species dietary composition and dominant prey species. Secondary objectives included: (1) quantifying the potential dietary overlap between Atlantic cod and three non-cod gadoids in 3Ps where their spatial distributions overlap in the spring and investigating whether the non-cod gadoids were competing with adult Atlantic cod, as in other regions (Renaud et al. 2012); (2) investigating intraguild predation and whether non-cod gadoids were preying upon the early life stages of Atlantic cod, which has been observed in other regions (Helser et al. 1995, Temming et al. 2007); and (3) analyzing diet similarity data in relation to spatial co-occurrence data in order to understand potential competitive interactions, using these results to potentially help explain degrees of similarity or lack thereof.

1.3 Methods

1.3.1 Sample Collection

Acoustic bottom trawl surveys were carried out in late April to late May from 2012-2014 aboard the RV *Celtic Explorer*. The survey used an acoustic transect design. This vessel used a scientific echo sounder (Simrad EK60 at frequencies of 18, 38, 120, and/or 200 kHz) that in the context of this study was used to both collect and quantify acoustic target information and direct trawl fishing sets towards signals characterized on echograms by experts as ‘gadoid’ with reference to prior gadoid signal (mostly Atlantic cod) (e.g. Rose 1992, Rose 1993, Knickle and Rose 2012). A total of 26 acoustic-directed fishing sets, occurring over a range of depths on the

shelf and shelf slope, were completed in 2012, 8 in 2013, and 27 in 2014. The locations of these sets are mapped in Figure 1.3. In 2014, 7 fishing sets from NAFO Division 3O, very close to the 3OP border, were included in analyses because fish caught in these sets were occupying similar habitats as the adjacent 3Ps region. In 2012 and 2014, a Campelen 1800 shrimp trawl (Walsh and McCallum 1997) was used, and in 2013 a Grand Overture Verticale (GOV) trawl (ICES 2012) was used. All sets' durations, dates, times, locations, fishing depths, and bottom temperatures are provided in Table A.1.

After the completion of a fishing set, all net contents were separated, species were identified and weighed separately, and study fish species were sampled on board. Each stomach sample was individually bagged, accompanied by a unique identification tag, and frozen whole (-18° C) for analysis in the laboratory. At sea, individual total length, sex, whole weight, gutted weight, and liver weight were recorded for all samples. In sets where the number of fish caught was less than 50, all intact stomachs were sampled. In most cases with larger sets, a length and sex stratified subsample of 30 to 60 individuals was taken. Using the original catch data as a guide, I chose a smaller number of samples to represent a scaled down version of the larger catch collected. I used length bins to simplify larger catches and included at least one male and one female from each length bin (1-3 cm bins). The subsample was a smaller proportion of the same length frequencies in the original sample. A unique identification tag number for each sample allowed it to be linked to life-history data from each fish and oceanographic data from the set in which the fish was caught. Based on within-set prey type accumulation curves created using randomizations of prey incidence data from stomachs collected (Gotelli and Colwell 2001), it was determined that these within-set subsamples were sufficient to reveal the majority of

potential prey species locally available to all four species (Figure A.1a-d). Randomizations were undertaken using *EstimateS* version 9 software (Colwell 2013).

Sampling was largely targeted towards the shelf slope region (exclusively so in 2014 given the survey design targeting a variety of shelf slope habitats), at depths ranging from 71-346 meters, given the distribution of gadoid signal from the fisheries acoustics (Figure 1.3). This pattern was also reflected in multi-year survey data on the spatial distributions of these four gadoid species collected by DFO, where in spring, their spatial distributions overlap largely along the edges of the shelf and on the shelf slope (Figures 1.4a-d); only Atlantic cod occurs frequently on the shallow shelf. It was hypothesized that in sets with co-occurring gadoids, diet overlap would be higher, as these fish would have access to a more similar prey community (Cushing 1974). In all three years, because fishing set locations were largely based on what was detected by the fisheries acoustics equipment, fishing effort was allocated mainly to locations where gadoid signal was present.

In all three cruises combined, 2404 haddock, 972 pollock, 6171 silver hake, and 2747 Atlantic cod were caught. Fish with everted stomachs were excluded from sampling, and in sets with very large numbers of one or more target species, stomachs were retained from a subsample of the catch. Stomach content analyses were performed on a subsample of 476 haddock, 212 pollock, 588 silver hake, and 1681 Atlantic cod. The higher proportions of Atlantic cod stomachs analyzed stem from the fact that they were targeted for focused investigations during the 2012 survey. For statistical analyses, empty stomachs were omitted, leaving 448 haddock samples, 196 pollock samples, 419 silver hake samples, and 1522 Atlantic cod samples (Table A.2).

1.3.2 Stomach Content Analyses

In the laboratory, individually tagged stomachs were dissected per stomach sampling protocols outlined in Cook and Bundy (2010). Stomach contents were examined under a dissecting microscope, and prey items were identified to class, order, or family level. When possible, especially for finfish prey, species level identification was attempted. Following identification, prey as well as non-food items were counted and weighed. Most prey fish were identifiable to species level using otoliths. Frequently encountered fish species were individually coded and rare or unidentified fish were coded as "other fish". In cases where otoliths, but no enumerable fish skeletons were present, the greatest number of either right or left otoliths was used to determine the number of fish consumed and the prey wet weight was recorded as the mass of skeletal fragments and otoliths. In the case of heavily digested crustaceans, such as euphausiids, numbers were estimated by counting pairs of eyes (Pinkas et al. 1971). For stomachs containing large numbers of one prey type, for example ostracods, a count of "100+" was used.

When considering overall diet trends, contents were categorized into one of four groups: finfish (capelin, sandlance, and other fish), benthic (sea stars, polychaete worms, crabs, gastropods, bivalves, and other benthic invertebrates), benthopelagic (shrimp, euphausiids, hyperiids, other amphipods, and other small benthopelagic invertebrates), and other prey types (unidentified crustaceans, plant material, and other non-food items).

1.3.3 Statistical Analyses

Data matrices (stomach sample rows by prey type columns) were analyzed using the statistical package Plymouth Routines In Multivariate Ecological Research (PRIMER, version

6.1.15). Year, set, depth, binned depth range, temperature, binned temperature range, length, and length class were recorded for all samples. Binning was included to determine if overlap changed when binned data were used versus continuous depths or temperatures. Additionally, when depths and temperature were binned into ranges, these were more easily analyzed in PRIMER.

First, the wet weight data of all prey items found in each stomach sample were standardized, expressing each prey type as a percentage of the total content weight. This is more an ecological standardization, rather than a statistical one. Next, Bray-Curtis similarities (Clarke and Gorley 2006) were calculated between every pair of samples. Over 3.3 million pair wise comparisons were calculated. This similarity can be between S = 0 (no prey items in common) and S = 100 (composition of all prey items is exactly the same in two stomachs). Using standardized wet weights and comparing similarity in composition rather than raw prey weights was advantageous as some of the prey categories were not comparable by wet weight, as heavier prey items would be emphasized and would minimize the role of smaller, lighter prey items in the sample. Conversely, standardized weights were chosen over numbers of each prey item because numbers put more emphasis on smaller, more abundant prey items and would minimize the role of larger, heavier prey items. This study used biomass as the unit of measure within diet analyses because it is a more direct metric of energy consumed by the predator, rather than numbers of prey that can vary in size and abundance by orders of magnitude. It is important to note that sets were incorporated as a factor in analyses because fish sampled within a set are not considered independent replicates.

From this matrix, a two-dimensional ordination plot was created using non-metric Multi-Dimensional Scaling (MDS). This ordination plot (Figure 1.5) is a visual configuration of all stomach samples based on rank similarities calculated from content composition. The most

similar pair of samples has the lowest rank, 1, and the most dissimilar has the highest rank, $n(n-1)/2$ (Clarke and Warwick 2001). The MDS plot is unitless and places samples with more similar composition closer together spatially than samples that are more different, and therefore illustrates the dissimilarity among the diets of the 4 species, and diet consistency intraspecifically in 2-dimensional space.

Next, the same resemblance matrix was used to run an Analysis of Similarities (ANOSIM). ANOSIM allows for the use of one or more factors to test the null hypothesis that there are no differences in stomach content composition among the four predator species (Clarke and Gorley 2006). For this study, a two-way nested ANOSIM was used to test for differences among species grouped within sets and for differences among sets across all species caused by area and/or year effects.

In a two-way nested ANOSIM, two null hypotheses exist:
H1: there are no diet differences among sets across all species groups
H2: there are no diet differences among the diets of the four species grouped by set

A two-way crossed analysis requires all species to occur at all levels of a second factor. Therefore, it could not be used to compare diets among sets from this dataset because not all species occurred in every set, but it could be used to investigate differences in diet among different temperature ranges. A two-way crossed ANOSIM tests for species differences while allowing for the possibility of block effects. Conversely, it tests for block differences while allowing for possible species effects.

A two-way crossed ANOSIM also tests two null hypotheses:

H1: there are no diet differences among temperature ranges, allowing for species effects

H2: there are no differences among the diets of the four species, allowing for temperature effects

A global R-statistic, individual R-statistics for each pairwise test, and associated significance values for all test statistics were calculated in ANOSIM. R was calculated by subtracting the average rank similarity of all replicates within a factor from the average rank similarity between all pairs of replicates between different factors and dividing that number by n(n-1)/4.

$$R = \frac{(r_B - r_W)}{n(n-1)/4}$$

Theoretically, in cases where no differences in diets exist, R is equal to 0 because the average rank similarities within and between species are equal. Typically, R>0 (maximum = 1) because it is more likely that ranked similarities between samples of different species will be larger than those within a species as degree of similarity and rank similarity are inversely proportional. An R close to -1 is rare because that would mean similarities between species greatly exceed those within a species. In complex ecosystems, fine scale or more localized interspecific interactions are often obscured by interactions across the entire system (Tylianakis et al. 2008); ANOSIM attempts to resolve this by calculating R-statistics and associated significance levels for all pairs of predator species to supplement the global R.

PRIMER's Similarity Percentages (SIMPER) routine was used to quantify how much individual prey types contributed to the overall Bray-Curtis diet dissimilarity between two groups of samples and which prey types contributed to diet similarity within a group (Clarke and Gorley 2006).

For these data, SIMPER for a two-way crossed layout was used because in a one-way test, differences among species can be confounded with differences among sets. The two-way SIMPER can bypass such effects by removing the 'block', i.e. spatiotemporal, effect (Clarke and Gorley 2006). To do this, dissimilarities among species and similarities within a species were calculated from the same block and then averaged across all blocks. As in the ANOSIM two-way crossed analysis, all species had to occur in combination with all levels of the block factor. The factor that satisfied this was bottom temperature grouped into five 2°C bins from -0.6°C through 8.7°C. After computing the average similarity within and dissimilarity between species, this average was broken down into contributions from each prey type. If a prey type contributed consistently to interspecific dissimilarity, the ratio between its average contribution and standard deviation would be large, making it a strong discriminating species. The same is true for prey types contributing consistently to intraspecific similarity, and are said to typify the diet (Clarke and Gorley 2006).

In addition to the aforementioned multivariate analyses, patterns in diets among species, years and length classes were also graphed in SigmaPlot to illustrate interannual variability and changes in predator diets with ontogeny.

1.4 Results

1.4.1 Atlantic Cod

Atlantic cod had the least consistent diet of the four species (S = 16.67%) across all temperature ranges, and was found to consume prey items from all four broad prey type groups (Figure 1.6). When looking at diets in relation to gadoid body size (Figures 1.7a-d) there were some changes with increasing length, with medium sized cod (30-65 cm) eating a higher

proportion of fish, and large cod (> 65 cm) eating more benthic organisms, namely crab (Figure 1.7a). Binning length data was attempted in formal analyses in PRIMER, but there were insufficient data to bin, and the sample sizes were too small for the analyses to run properly. Figure 1.5 is meant to illustrate overall variability and similarity among species. Variation in diet by length was considered important (Figure 1.7a-d), and length explained some of the variability that was concealed within length-aggregated analyses (Figure 1.6).

As a result of its apparent generalist diet, no prey types could be considered typical as they all had very low contribution to standard deviation ratios. Various benthic and benthopelagic invertebrates, including molluscs, echinoderms, and amphipods, were the most abundant prey and contributed to almost 49% of diet similarity. Because of the low consistency in diet, many other prey types had large average abundances including sandlance, crabs, brittle stars, other fish, euphausiids, and hyperiids. These 7 types explained more than 90% of the intraspecific similarity in cod diets (Table 1.1a).

Despite sampling a relatively consistent length range across years, interannual variation in Atlantic cod diet contributed heavily to the small S value (Figure 1.8). For example, in 2012, *Chionoecetes* and *Hyas* crab species, brittle stars, and sandlance accounted for 51% of cod diet by wet weight. In 2013, crabs and brittle stars made up 55% of cod diet by wet weight; while sandlance was almost completely absent from cod stomachs in that year. In 2014, sandlance and other fish comprised over 70% of the wet weight of cod diet. Capelin (*Mallotus villosus*) accounted for less than 9% of consumed prey in any of the three years for cod, although it was a dominant species in silver hake diet in 2012 and pollock diet in 2014.

1.4.2 Haddock

Haddock was largely (~80%) benthivorous (Figure 1.6) and had the least variable diet of the four study species with an intraspecific diet similarity of 45.38%. In haddock, finfish prey items were rarely found in the stomachs of fish less than 60 centimeters in length (Figure 1.7b). Like cod, various benthic and benthopelagic invertebrates were the most abundant prey type in haddock, contributing to over 40% of the diet similarity. Other, less common invertebrate species combined to have a strong presence in haddock diet in all years. Brittle stars and polychaete worms described over 56% of the total similarity. However, these prey items were not consistently found in the diet as the ratio of diet contribution to standard deviation never exceeded 0.80 (Table 1.1b).

Despite significant inter-annual variation, brittle stars were a dominant prey type in haddock in all years (Figure 1.9). Polychaete worms were also consistently present and appeared in larger quantities with each successive year, and exceeded the wet weight of brittle stars in the diet in 2014. Haddock diet was more similar to cod (14.64% similar) than to pollock (2.72% similar) or silver hake (3.05% similar), as the latter two species had very small quantities of benthic prey types in their gut.

1.4.3 Silver Hake

Silver hake had a level of intraspecific similarity of 32.05%, and almost all of the similarity was described by two prey types: benthopelagic euphausiids and miscellaneous fish (Figure 1.6, Table 1.1c). Silver hake diet was only dominated by finfish prey in 2012, specifically capelin. Silver hake exhibited increased piscivory with increasing length, and finfish were a dominant prey item by wet weight in individuals in excess of 40 centimeters and silver

hake over 50 cm in length sampled by CFER consumed finfish prey exclusively (Figure 1.7c). A trend of decreased piscivory with increasing latitudes was documented by Helser et al. (1995) (Figure 1.13).

The majority of the diet consisted of euphausiids in the other two years (Figure 1.10). Despite only two prey items contributing largely to the diet of silver hake, neither had a large enough similarity to standard deviation ratio to be considered a typifying prey species (Table 1.1c), and this may be because there is variation among years with regards to how much wet weight euphausiids and other fish contributed to diet. Although thorough sampling was attempted, data for analyses for this species were scarcer because of a high proportion of everted and empty stomachs, especially of larger individuals (Table A.3). Fish with everted stomachs were not collected for sampling.

1.4.4 Pollock

Pollock had the second lowest intraspecific diet similarity (26.03%), and like cod, none of the major prey items were found in consistently large abundances. Data from pollock for two years gave sandlance, hyperiids, euphausiids, and capelin as dominant species that contributed to over 90% of the intraspecific similarity; invertebrates dominated the diets of smaller pollock while finfish prey dominated the diets of larger pollock (Figure 1.7d, Table 1.1d).

3Ps pollock was more piscivorous than the other species overall (Figure 1.7d, Figure 1.11). Like silver hake, this species tended toward increased piscivory with increased body length, but finfish prey was found in almost every 5 centimeter length class (Figure 1.7d). Of the four species, it was the only one to predominantly consume fish in 2013 (Figure 1.11). Sandlance was by far the most abundant prey item in 2013, but was replaced by a similar percentage of

capelin in 2014, and composed almost 90% of the diet by wet weight. The percentage of sandlance in 2014 was much lower. Pollock diet was more similar to silver hake than to haddock.

1.4.5 Interspecific Functional Overlap

The two-dimensional ordination plot created through non-metric Multi-Dimensional Scaling (Figure 1.5), showed that there was some overlap among the four species, but there was a lot of variability within some species, particularly Atlantic cod. Generally, Atlantic cod and haddock were clustered closer together, with pollock and silver hake showing more pairwise overlap. The stress level of the two-dimensional MDS plot was 0.14, which provides a sufficiently accurate depiction of the data. A low stress level here denotes that the data are represented effectively in two dimensions and that a three-dimensional representation is not necessary. The degree of overlap illustrated by the ordination plot was cause for additional quantitative testing using ANOSIM and SIMPER routines.

A two-way ANOSIM with set nested within species rejected the first null hypothesis that there were no spatial or temporal effects: among sets or years ($R = 0.288$, $p < 0.001$). The second null hypothesis that there were no differences in prey composition among the four predators' diets was also rejected ($R = 0.353$, $p < 0.001$). Significant differences were also obtained from the two-way crossed design between species and temperature ranges (species $R = 0.074$, $p < 0.001$; temperature $R = 0.123$, $p < 0.001$).

The six pairwise tests for set nested within species yielded large R-statistic values that were significantly different from the null distribution with or without corrections for multiple tests ($p < 0.001$), with the exception of the cod-haddock test ($R = -0.123$, $p = 0.985$). This R value suggests a degree of interspecific diet overlap between these two species. The two-way

crossed ANOSIM (species, temperature ranges as factors) yielded a similar result between these two species ($R = -0.079$, $p = 1$). The R-statistic was non-significant, so we were unable to reject the null hypothesis that there is no difference between the two diets.

The two-way crossed SIMPER routine revealed that interspecific diet similarity was very low for all pairs of species (Tables 1.2a-f). Silver hake diet was more similar to pollock than to the other two species, but still had a dissimilarity of 87.83% because silver hake diet was dominated by euphausiids and pollock diet by sandlance (*Ammodytes dubius*) and hyperiids (Table 1.2f). Atlantic cod and haddock had the most similar diets, but still had an average dissimilarity of 85.36%. Discriminating prey items and their contributions are listed in Table 1.2a. Haddock and pollock were the most dissimilar at 97.28% (out of a possible dissimilarity of 100%). The discriminating prey types by contribution to dissimilarity are listed in Table 1.2e. When sets were incorporated as a factor into the model, it did not change the result of the analyses and reduced the statistical power of the analysis. When data were simplified into average diet per species by set, the sample size was too small for analyses to be successfully performed.

Figure 1.12 shows that in 2014, when CFER attempted multiple series of depth stratified sets, almost all cod were caught in waters shallower than 110 meters, while silver hake was the dominant species for all sets deeper than 155 meters. Haddock and pollock were caught in sets between these two depths. If the species were not occupying the same depths, they may not have had access to the same prey types, contributing to low interspecific overlap.

From samples collected in 3Ps in April and May, juvenile Atlantic cod were not found in the stomach contents of any of the four species, and from the samples collected there was no

evidence of intraguild predation. This was investigated to address the second objective of this study.

1.5 Discussion and Conclusions

Given recent changes in ocean conditions, species movements and increased abundances of non-cod gadoids in NAFO Subdivision 3Ps, the main goal of this study was to investigate and quantify predation and species interactions among four gadoid species in southern Newfoundland waters where their distributions overlap in the spring. Based on these data, there was no statistically significant diet overlap among most of these gadoid species overall. The implication of this result is that interspecific competition appears to be low at the sampling locations in the spring and therefore the dynamics of one species do not seem likely to be regulated by interspecific competition at this time of year.

One explanation for the low degree of dietary overlap may be due to species inhabiting different depths even in the same geographical location. Depth stratification of gadoid species may partly account for interspecific diet differences, as different prey species are available at different depths (e.g. crabs: Mullowney et al. 2012). This finding may provide an explanation for why dominant prey items are different in each diet and competition as measured by diet overlap appears to be low among these species, some of which are part of the same functional group. Another explanation may be due to shifts in diet as size increases. Because the sample size was too small to compare diets by length bins in PRIMER analyses, continued studies of these shifts in 3Ps may provide interesting findings and potentially provide more insight on diet overlap in this region.

In order to provide a wider context for the findings of my research, they can be compared to studies of ecosystems farther south, where food habits are comparatively better studied (Durbin et al. 1983, Waldron 1992, Garrison and Link 2000a, Laurinolli et al. 2004, Smith et al. 2007, Link et al. 2009, Cook and Bundy 2010). Food habits data help us investigate species interactions and provide insight into a major cause of natural mortality: predation. Furthermore, models that consider trophodynamics can help answer questions regarding system-level properties of finfish communities in transition (Link and Almeida 2000) and can reveal obstacles encountered by populations recovering from overexploitation (Nye et al. 2013). Overall, these data can be used to better understand the stocks (Ulltang 1996), which is necessary in the context of managing the existing 3Ps cod fishery (DFO 2015a). A difficulty with comparing studies, however, is that they may differ in the life stage or size range being examined. For example, over the past four decades, the lengths-at-age of silver hake on the Scotian Shelf have decreased (DFO 2013). In such circumstances, diet descriptions for aggregated lengths that change over time may be more reflective of changes in size structure rather than changes in diet, as smaller individuals tend to consume more invertebrates. This, again, emphasizes the utility of Figure 1.7, where size-based changes are evident and quantified. It would be useful to continue to collect paired diet and predator size information, although size-at-age data for silver hake in 3Ps has not yet been collected.

The dominant prey types being consumed by the four species were different and no prey types typified a single species' diet. The implication of this finding is that valuable offshore snow crab fisheries may not be negatively impacted by increases in non-cod gadoid abundances; however, we found that of the Atlantic cod that were sampled, crab, both commercial and non-commercial species, made a large contribution to their diet, especially in 2013. Conversely,

predation by cod at this time of year did not appear to exert a large amount of pressure on the 3Ps capelin stock, but silver hake and pollock were significant consumers of this species in 2012 and 2014, respectively (Figure 1.10, Figure 1.11). Notably, there was no evidence from the stomach content analyses of intraguild predation or that these species are preying upon early life stages of Atlantic cod in the spring. This information fills a key gap in understanding trophic relationships in this area and how they affect cod productivity (DFO 2015a). Continuing multi-species surveys to lengthen the time series (potentially in collaboration within existing DFO surveys) and adding surveys at other times of year would give more insight into gadoid diets within the area.

Atlantic cod was the most thoroughly sampled species in all three years and was sampled across a larger spatial range. This potential sampling bias (as Atlantic cod has the widest geographic range at this time of year; Figure 1.4d) paired with a more generalist diet (S = 16.67%) may have contributed to a potential for more overlap in diet composition with other species. However, the average dissimilarity was 85.36% and this value is too large to conclude that the two diets have a biologically significant overlap.

Analysis of Atlantic cod diet data showed that the diet was not consistent among years and overall generalist. This species consumed prey characteristic of all areas of the water column. It can be concluded that while cod may consume prey items that are more energetically valuable and desirable (e.g. capelin, DeBlois and Rose 1996, Rideout and Rose 2006), in an ecosystem experiencing declines in this species (Tretyakov 2013, Buren et al. 2014) cod was found to be the most opportunistic generalist predator of the four species. Cod was also found to be a generalist predator in studies from Cape Hatteras, NC to Nova Scotia (Link and Almeida 2000). In a late summer study conducted in Placentia Bay, Atlantic cod were found to consume predominantly capelin and hyperiid amphipods, with echinoderms increasing in the diet in the

fall (Lawson and Rose 2000). Given that Atlantic cod are generalists, they presumably have the ability to switch to new prey items if others become scarce, there is more competition for a particular type of prey, or if predator-prey interactions uncouple due to climate (Winder and Schindler 2004). This is advantageous because if new gadoids become established in 3Ps, cod would be resilient if abundances of certain prey decrease, which has been shown in other systems (Shaw et al. 2008). Similar shifts to new prey types have been observed in other ecosystems (Lee and Khan 2000, Link and Garrison 2002).

When looking at the composition of cod diet in more detail, however, it appears that 3Ps cod in spring have different food habits than stocks farther south. For example, crab species, which dominated the diet of 3Ps cod, especially in 2013, never exceeded 15% of the diet by wet weight in Atlantic cod caught along the northeast coast of the United States (Link and Garrison 2002). In those more southern ecosystems, crustaceans, amphipods, and pandalus shrimp were the dominant prey types for fish less than 50 centimeters long, while herring, silver hake, and other gadoids made up the majority of stomach contents of larger fish. In a recent study of Newfoundland cod stocks by Kyle Krumsick of CFER (unpublished), it was found that crab species were not a significant contributor to diet, although the methods dictate that only crab with carapace widths less than or equal to 40 mm were described as being an appropriate size range for cod consumption (unpublished data). However, the present study found that the gut contents of some cod longer than 45 cm contained crabs with carapace widths greater than 40 mm.

While diet composition is highly related to the resident prey community, the food habits of Atlantic cod in southern Newfoundland waters are certainly different from those in the north and ecosystems farther south. For example, on the St. Pierre Bank, sandlance has been

considered an analogous prey item to capelin in the diet of the more northern cod stocks (Lilly and Fleming 1981), which may explain why there was such a large proportion of this prey in 2012 and 2014. The results from this study also differed from cod diet data from 3Ps in previous decades. When these diet data were compared to those from the 1980s and 1990s, there were many differences in the stomach contents. It was observed that a diet dominated by cod, redfish (*Sebastes sp.*), and capelin prey, shifted to one dominated by sandlance and crab species (Koen-Alonso et al. 2013). These observations were a reflection the spatio-temporal overlap between cod and its prey and of cod's ability to adjust to changing prey availabilities (Cushing 1974, Link and Garrison 2002).

Haddock had a more consistent diet relative to the other species, although diet consistency can be problematic if the abundance of a major food item decreases, as specialists are more susceptible to changes in prey composition (Shaw et al. 2008). However, as haddock was largely a benthic consumer, it fed on a different suite of prey species than was consumed by the other gadoids in 3Ps. It can be concluded that because haddock occupy a different niche than other gadoids in this region, that their food sources are not acutely threatened by competition with emerging gadoids in southern Newfoundland waters in spring.

Haddock diets in 3Ps had some differences from haddock sampled farther south, but were similar in that echinoderms were found as dominant prey species regardless of ontogeny (Tam et al. 2016). Cook and Bundy (2010) complied data from a wide range of survey times and years in the Scotia-Fundy region and found that while haddock did consume many benthic organisms, other gadoids composed almost half of haddock diet by weight. In comparison, no gadoids were found in the stomachs of haddock from the CFER spring surveys, although the upper range of sampled haddock was 86 centimeters, which is within the size range of haddock that exhibits

piscivory. Finfish prey only accounted for about 13% of haddock diet by weight, and was mostly small numbers of sandlance and redfish. The difference may be the result of sampling season, the availability of benthic invertebrate prey, or due to the fact that in this ecosystem, other gadoids have not yet reached abundances of young individuals where predation from haddock is common. If this is the case, and if pollock and silver hake were recruiting to this area, we would expect to see increased instances of intraguild predation with each passing year. Additional sampling would be needed to find if this pattern emerges, or if it occurs at other times of the year, and if it does, this could have negative implications for the rebuilding 3Ps cod stock.

Silver hake in this study was found to be a more pelagic predator, consuming some finfish, but mostly euphausiid species. This result was similar to those found by the food web dynamics program in Woods Hole, Massachusetts (Link and Almeida 2000) and consistent with an increasing percentage of invertebrate prey in northern systems where invertebrates dominated diets on the Scotian Shelf (Helser et al. 1995, see Figure 1.13). Changes in diet with fish length within this area (Figure 1.7a-d) suggest that comparisons among regions should consider fish length as well as species identities. This study also agrees with the findings of Waldron (1992), who found that euphausiids make up the majority of the diet of silver hake on the adjacent Scotian Shelf. However, this finding is the result of analyzing small silver hake stomachs and with the study of more large fish, there could be a potential diet shift (Cook, personal communication).

From what was analyzed, it was found that silver hake caught in 3Ps was less piscivorous over the time series than populations in other areas of their range based on the literature (Waldron 1992), but this may be due to the lack of stomach samples from larger fish, as piscivory tends to increase with increasing fish size (Durbin et al. 1983, Garrison and Link

2000b), which was observed in the size range that was sampled. In 2012 and 2014, fish prey composed at least 50% of the diet by wet weight for fish greater than 30 centimeters and greater than 35 centimeters, respectively. This tendency toward increased piscivory with increased length was expected for this species; as it has been described farther south (Waldron 1992, Garrison and Link 2000b).

Silver hake has also been recognized for being both predator of and prey for cod, pollock, and other hakes (Almeida 1978, Nye et al. 2011). In our analyses, these interactions were not observed. None of the species of interest were found to prey upon the others. Due to the sampling being carried out exclusively in the spring and the absence of larger, more piscivorous size classes (Durbin et al. 1983, Garrison and Link 2000b), it cannot be determined if, like with haddock, this is an effect of sampling time, size structure of the catch, or if 3Ps gadoids exhibit different predatory behaviour compared to stocks farther south. Future survey design should incorporate sampling protocols that target these questions related to silver hake.

Within this study, silver hake also had by far the highest percentage of empty stomachs at almost 29% (Table A.3). The large percentage of empty silver hake stomachs may have been because they have been found to move prey through their gut more quickly than other gadoids (Bowman 1981, Durbin et al. 1983), or because of their tendency toward regurgitation and stomach eversion when brought up from depth (Bowman 1981, Bowman 1986). Eversion was most prevalent in larger silver hake, suggesting that the latter was a factor. Silver hake was caught, on average, at the greatest depths of the CFER surveys (Figure 1.12). There was a broad size range of hake caught, however almost all large individuals were unsuitable for analysis because of stomach eversion, which left a critical gap in the data set. As a result, even sets in which hundreds of silver hake were caught, only a narrow size range was sampled, and of this

small subsample, sometimes less than half contained prey items. For these reasons, many of the sets could not capture the full size range of this species.

Pollock was easy to analyze as many of the stomachs were full of readily identifiable prey. Pollock from this region were heavily piscivorous in the spring, and a tendency toward piscivory increased with length. Carruthers et al. (2005) also observed this trend on the Scotian Shelf. In the present study, this species had the smallest sample size and the time series was shorter with only two years of diet data. In the first year, the diet was completely dominated by sandlance, and in the second year the diet was completely dominated by capelin. In data compiled from a number of studies on the Scotian Shelf and Bay of Fundy by Laurinolli et al. (2004), sandlance was found in almost all size classes of pollock above 25 centimeters. Given the infrequency of capelin on the Scotian Shelf (Frank et al. 1996), its absence from the diet in that study may be explained more by biogeographic limits of their potential prey rather than pollock prey preferences. Another difference between pollock from 3Ps and populations farther south is that large zooplankton was the second largest contributor to diet in the south, but was not a dominant prey type for pollock in 3Ps.

Because of large interannual differences in abundance, no prey types were considered typical or occurring consistently. Therefore, we are unable to draw conclusions about pollock diet using only two very different years of data. One thing that may be concluded with a degree of certainty is that if pollock increases in abundance along with silver hake, this may lead to the consumption of large quantities of finfish prey previously being preyed upon by larger size classes of Atlantic cod. Although this study found that cod are more generalist predators, the consumption of an energy rich food source by emerging non-cod gadoids may prove to be detrimental to the resident cod in areas where piscivorous species co-occur.

In 2013 sandlance was rarely found in cod stomachs, but it represented over 75% of pollock diet in that year. The opposite was true for 2014. And while capelin was not a dominant prey species in any year for cod, it was found frequently in silver hake stomachs in 2012 and pollock stomachs in 2014. This illustrated that while some finfish prey species were present, they were consumed by different predators in different years, and may be the result of the more mobile, pelagic nature of silver hake and pollock. As capelin has experienced a decline in 3Ps due to a shift southward (Carscadden et al. 2001, Rose 2005b), less are available for consumption, so more mobile species would be more likely to consume this decreasingly abundant species. It seemed that energetically valuable prey species (i.e. capelin and sandlance) were only heavily preyed upon by one gadoid predator in any given year. This supports the conjecture that, like cod, pollock and silver hake are opportunistic piscivores (Link and Garrison 2002), although some species may be more metabolically desirable. This study was limited in that there was a short time series with data from only one season and three years, and limited spatial extent and little interannual resampling of sets. As a result, a continued multispecies approach to address both spatial distributions and patterns of consumption would provide more information on trophodynamics and predator-prey interactions, as multiple years of diet data are important for gaining a good understanding of these dynamics.

It is apparent that changing ocean conditions, particularly a warming trend, are currently bringing more southern species into Subdivision 3Ps in the spring. Increasing numbers of finfish predators are of particular interest when they occupy the same functional groups as resident species. This is the case with silver hake and Atlantic cod. Due to the emergence of southern species (DFO 2015a), it was important to quantify competition and predation among these and the local cod stock, as these affect ecosystem structure and productivity and prey distributions

and abundances (Garrison and Link 2000a, Cook and Bundy 2010, Kempf et al. 2010, Albouy et al. 2011). These findings are not only important in fisheries contexts, but to increase knowledge of an ecosystem that is characterized as a faunal transition zone (Pinhorn and Halliday 1997) containing gadoid populations with feeding behaviours that differ from adjacent stocks.

Table 1.1a-d: Average intraspecific diet similarity based on Bray-Curtis and prey species in descending order of contribution to diet similarity within four gadoid species across all temperature bins (to a cut off of ≈ 90%).

a) Group Atlantic Cod
Average similarity: 16.67

Species	Av. Abund	Av. Sim	Sim/SD	Contrib.%	Cum.%
Other Inverts	20.85	8.16	0.37	48.94	48.94
Sandlance	11.18	1.89	0.16	11.35	60.29
Crab	10.35	1.60	0.16	9.61	69.91
Ophiurida	12.00	1.58	0.16	9.49	79.39
Other Fish	7.71	0.66	0.11	3.93	83.33
Euphausiidae	7.09	0.61	0.11	3.64	86.97
Hyperiidae	5.59	0.54	0.10	3.24	90.21

b) Group Haddock
Average similarity: 45.38

Species	Av. Abund	Av. Sim	Sim/SD	Contrib.%	Cum.%
Other Inverts	29.22	18.55	0.80	40.87	40.87
Ophiurida	33.75	16.28	0.75	35.88	76.75
Polychaeta	21.76	9.49	0.75	20.91	97.66

c) Group Silver Hake
Average similarity: 32.05

Species	Av. Abund	Av. Sim	Sim/SD	Contrib.%	Cum.%
Euphausiidae	53.22	26.94	0.66	84.06	84.06
Other Fish	15.10	2.61	0.17	8.14	92.21

d) Group Pollock
Average similarity: 26.03

Species	Av. Abund	Av. Sim	Sim/SD	Contrib.%	Cum.%
Sandlance	31.18	11.92	0.42	45.79	45.79
Hyperiidae	19.65	7.14	0.40	27.42	73.21
Euphausiidae	9.35	2.77	0.32	10.65	83.86
Capelin	13.46	2.01	0.15	7.72	91.58

Table 1.2a-f: Average interspecific diet dissimilarity based on Bray-Curtis and prey species in descending order of contribution to diet dissimilarity between six unique pairings of four gadoid species across all temperature bins (to a cut off of ≈ 90%).

a) Groups Atlantic Cod & Haddock
Average dissimilarity = 85.36

Species	Group Atlantic Cod Av. Abundance	Group Haddock Av. Abundance	Av. Diss	Diss/SD	Contrib.%	Cum.%
Ophiurida	12.00	33.75	19.43	1.29	22.77	22.77
Other Inverts	20.85	29.22	17.09	1.11	20.03	42.79
Polychaeta	2.88	21.76	12.87	1.01	15.07	57.87
Crab	10.35	2.84	7.11	0.48	8.33	66.19
Sandlance	11.18	0.39	5.36	0.37	6.27	72.47
Other	6.08	6.32	5.15	0.41	6.03	78.50
Other Fish	7.71	2.60	5.08	0.39	5.95	84.45
Crustacea	6.77	0.96	3.82	0.32	4.47	88.92
Shrimp	6.44	0.76	3.20	0.30	3.75	92.67

b) Groups Atlantic Cod & Silver Hake
Average dissimilarity = 89.00

Species	Group Atlantic Cod Av. Abundance	Group Silver Hake Av. Abundance	Av. Diss	Diss/SD	Contrib.%	Cum.%
Euphausiidae	7.09	53.22	25.92	1.17	29.13	29.13
Other Fish	7.71	15.10	10.42	0.57	11.70	40.83
Other Inverts	20.85	1.65	7.86	0.50	8.83	49.66
Hyperiidae	5.59	8.90	7.85	0.51	8.82	58.48
Sandlance	11.18	1.43	7.63	0.46	8.58	67.06
Ophiurida	12.00	0.00	5.57	0.40	6.26	73.32
Capelin	3.05	5.47	4.99	0.35	5.60	78.92
Crustacea	6.77	4.84	4.90	0.36	5.50	84.42
Other	6.08	6.35	4.79	0.37	5.39	89.81
Shrimp	6.44	2.16	3.94	0.32	4.43	94.23

c) Groups Haddock & Silver Hake
Average dissimilarity = 96.95

Species	Group Haddock Av. Abundance	Group Silver Hake Av. Abundance	Av. Diss	Diss/SD	Contrib.%	Cum.%
Euphausiidae	0.81	53.22	26.39	1.14	27.22	27.22
Ophiurida	33.75	0.00	16.13	0.97	16.64	43.86
Other Inverts	29.22	1.65	12.44	0.83	12.83	56.69
Polychaeta	21.76	0.55	9.77	0.77	10.08	66.77
Other Fish	2.60	15.10	8.01	0.46	8.26	75.03
Other	6.32	6.35	7.79	0.49	8.04	83.06
Hyperiidae	0.49	8.90	4.66	0.39	4.81	87.87
Capelin	0.10	5.47	3.76	0.30	3.88	91.75

d) Groups Atlantic Cod & Pollock
Average dissimilarity = 87.00

Species	Group Atlantic Cod Av. Abundance	Group Pollock Av. Abundance	Av. Diss	Diss/SD	Contrib.%	Cum.%
Sandlance	11.18	31.18	18.88	0.89	21.69	21.69
Capelin	3.05	13.46	9.13	0.52	10.50	32.19
Hyperiidae	5.59	19.65	8.94	0.57	10.28	42.47
Other Inverts	20.85	0.15	8.66	0.52	9.96	52.43
Other Fish	7.71	5.99	8.64	0.56	9.93	62.36
Crustacea	6.77	6.91	6.66	0.44	7.66	70.02
Euphausiidae	7.09	9.35	6.03	0.48	6.93	76.95
Other	6.08	6.57	5.52	0.42	6.34	83.29
Shrimp	6.44	6.74	5.00	0.36	5.75	89.04
Ophiurida	12.00	0.00	4.31	0.35	4.96	94.00

e) Groups Haddock & Pollock
Average dissimilarity = 97.28

Species	Group Haddock Av. Abundance	Group Pollock Av. Abundance	Av. Diss	Diss/SD	Contrib.%	Cum.%
Sandlance	0.39	31.18	16.57	0.78	17.04	17.04
Ophiurida	33.75	0.00	14.17	1.01	14.56	31.60
Other Inverts	29.22	0.15	12.15	0.95	12.49	44.09
Polychaeta	21.76	0.00	11.90	0.96	12.23	56.32
Other	6.32	6.57	10.30	0.60	10.59	66.91
Hyperiidae	0.49	19.65	8.41	0.55	8.64	75.55
Capelin	0.10	13.46	6.95	0.43	7.15	82.70
Other Fish	2.60	5.99	4.51	0.38	4.64	87.34
Euphausiidae	0.81	9.35	4.36	0.42	4.48	91.82

f) Groups Silver Hake & Pollock
Average dissimilarity = 87.83

Species	Group Silver Hake Av. Abundance	Group Pollock Av. Abundance	Av. Diss	Diss/SD	Contrib.%	Cum.%
Euphausiidae	53.22	9.35	26.18	1.25	29.81	29.81
Sandlance	1.43	31.18	15.82	0.75	18.01	47.83
Hyperiidae	8.90	19.65	14.06	0.80	16.01	63.84
Other Fish	15.10	5.99	9.75	0.53	11.10	74.94
Other	6.35	6.57	6.95	0.41	7.91	82.85
Crustacea	4.84	6.91	5.86	0.40	6.67	89.52
Shrimp	2.16	6.74	5.04	0.35	5.74	95.27

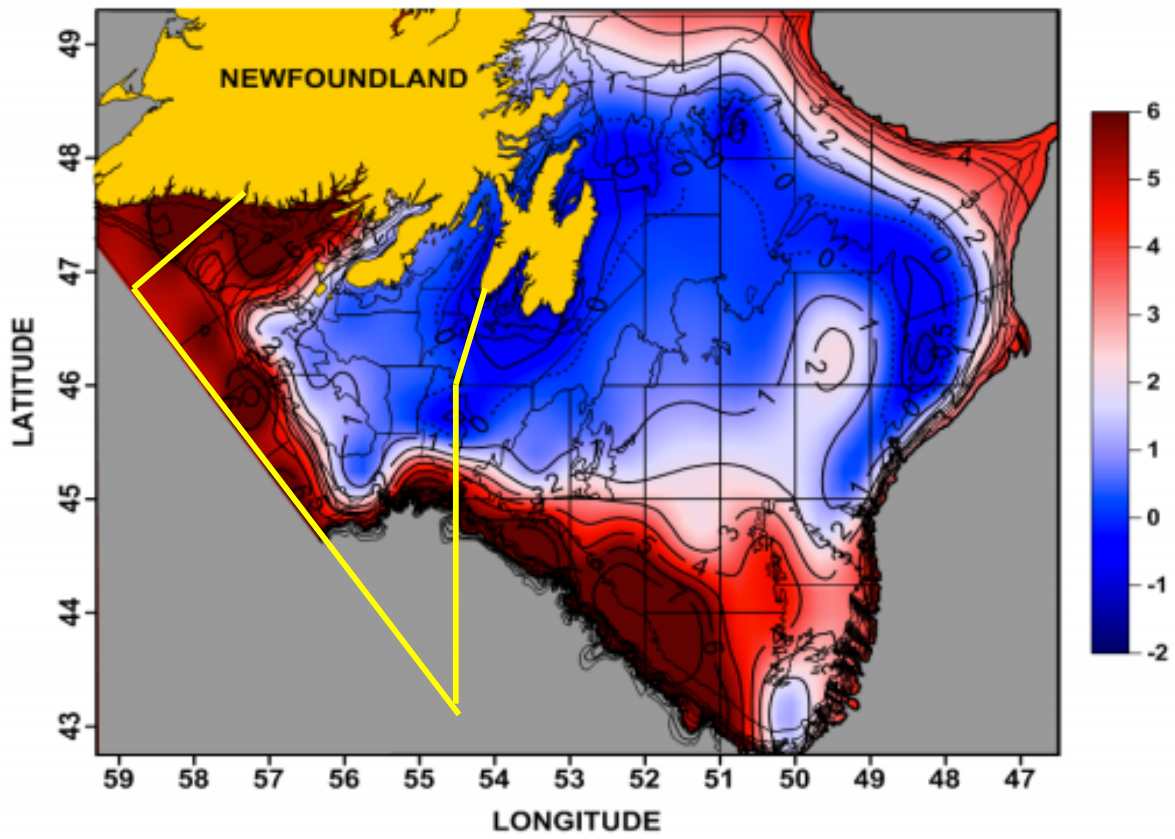

Figure 1.1a : Contour map of bottom temperature in degrees Celsius in NAFO Divisions 3PLNO in the spring of 2012. 3Ps is outlined in yellow. Bottom temperatures were above normal by about 1°C in 2012, which was a moderate decrease from conditions in 2011 (modified from Colbourne et al. 2013).

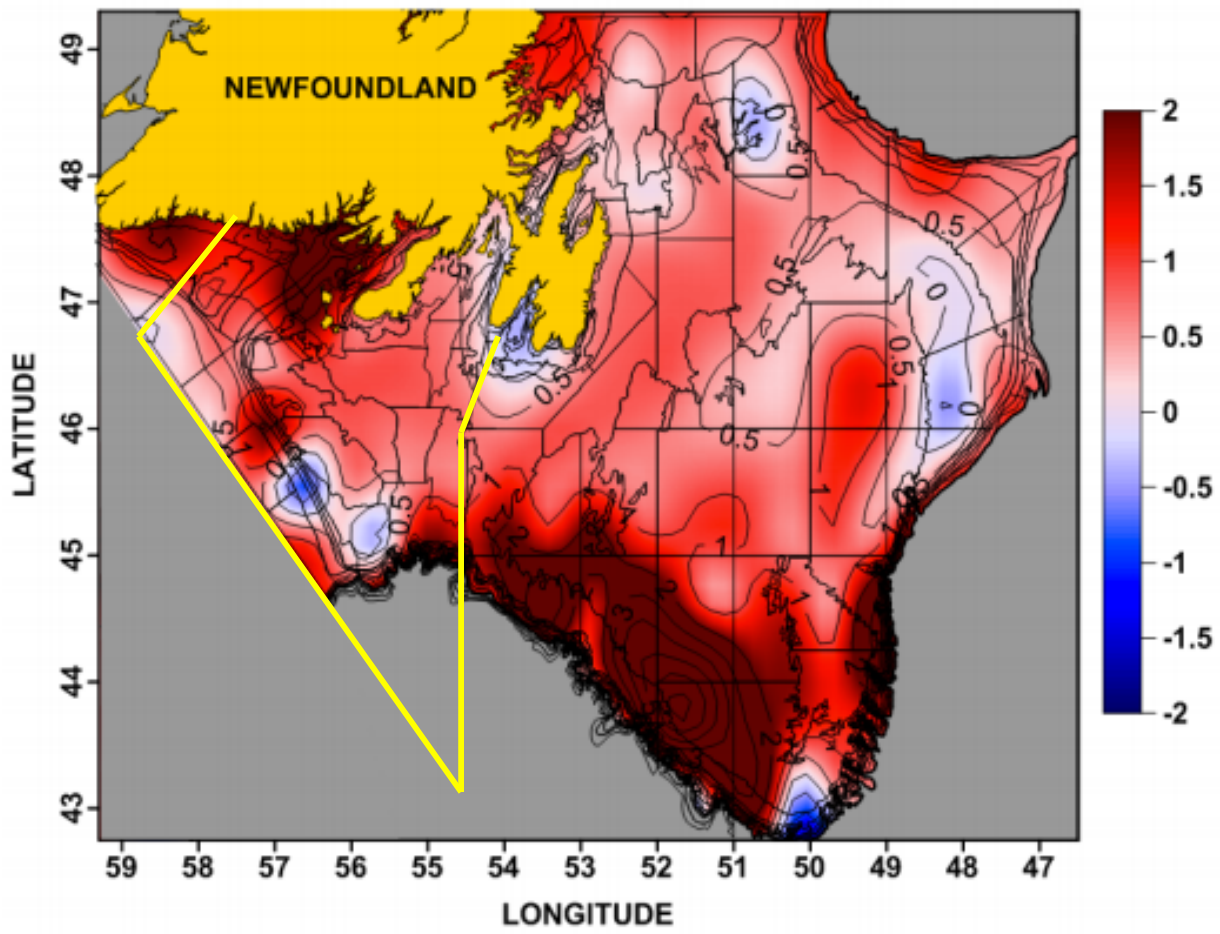

Figure 1.1b: Contour map of bottom temperature anomaly (1981-2010) in degrees Celsius in NAFO Divisions 3PLNO in the spring of 2012. 3Ps is outlined in yellow. Bottom temperatures were above normal by about 1°C in 2012, which was a moderate decrease from conditions in 2011 (modified from Colbourne et al. 2013).

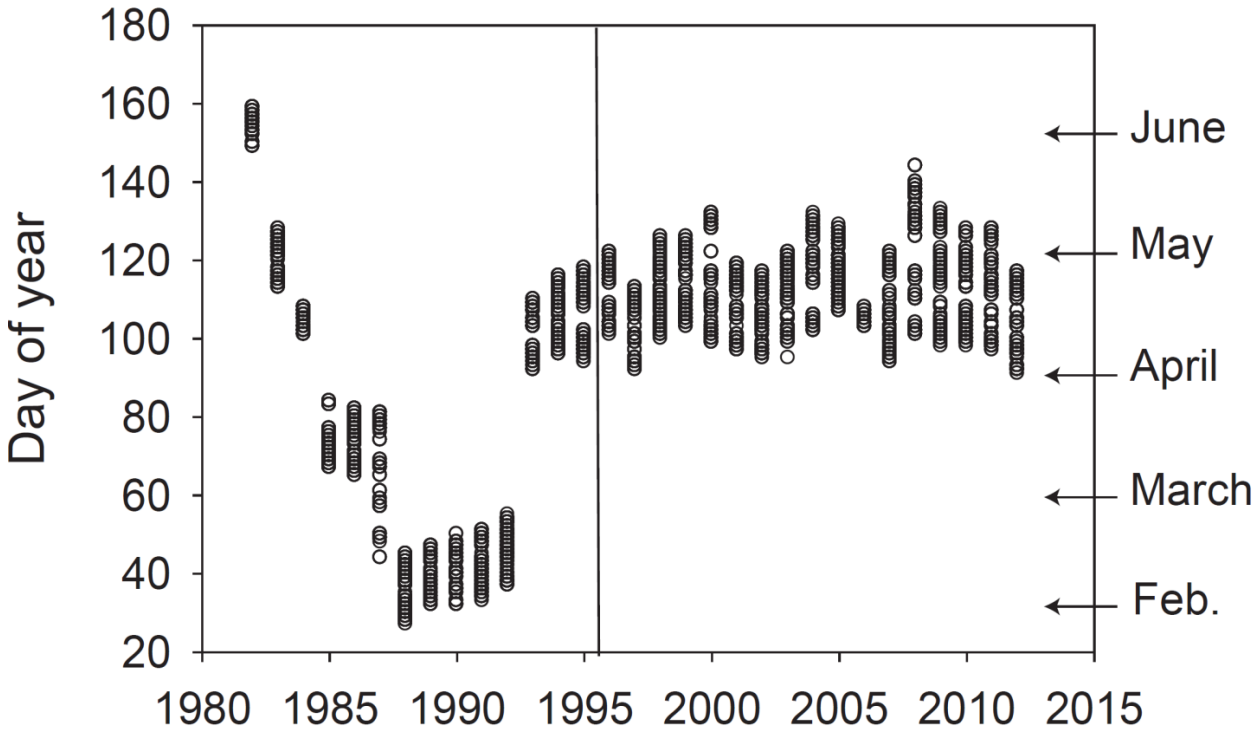

Figure 1.2a: Time series of DFO survey days in 3Ps. The survey began in April from 1993 onward (modified from Fisher and Koen-Alonso 2013).

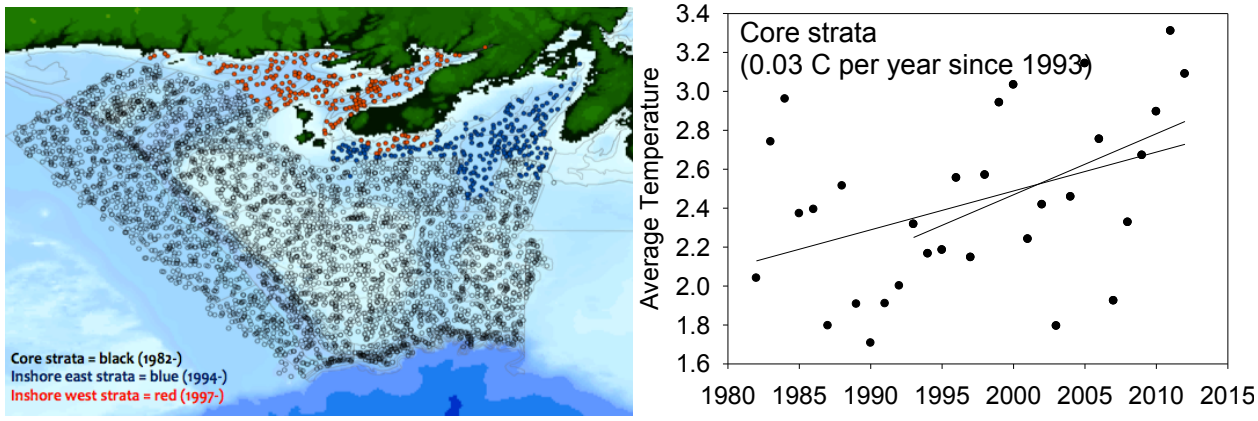

Figure 1.2b-c: NAFO Subdivision 3Ps core strata (black) depicted in b: DFO 3Ps spring survey sampling extent from 1982 and c: the average temperature increased by an average of 0.03°C per year in these strata from 1993-2012 (modified from Fisher and Koen-Alonso 2013).

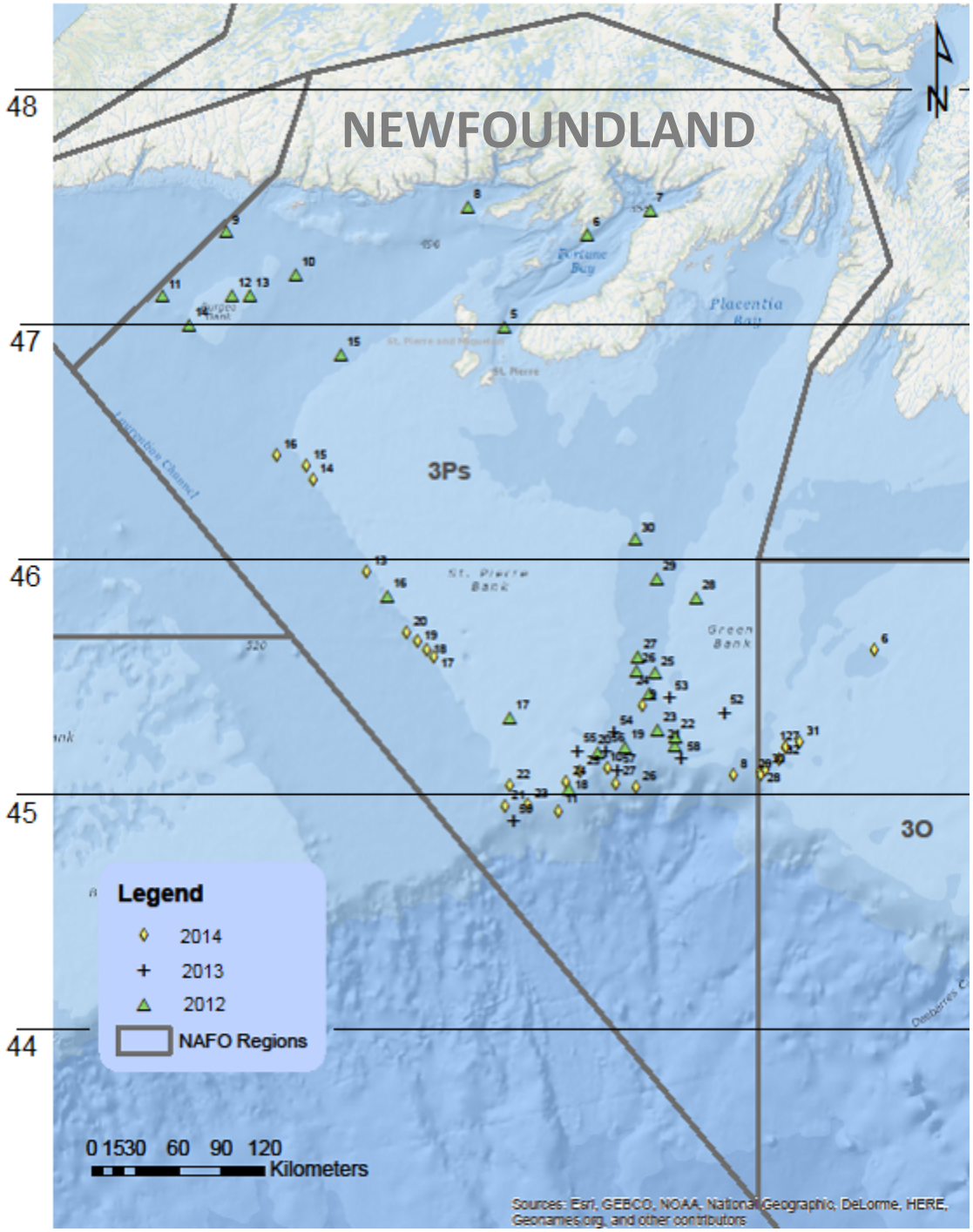

Figure 1.3: The study region, including NAFO Subdivision 3Ps, Division 3O, and CFER spring survey set locations from 2012-2014.

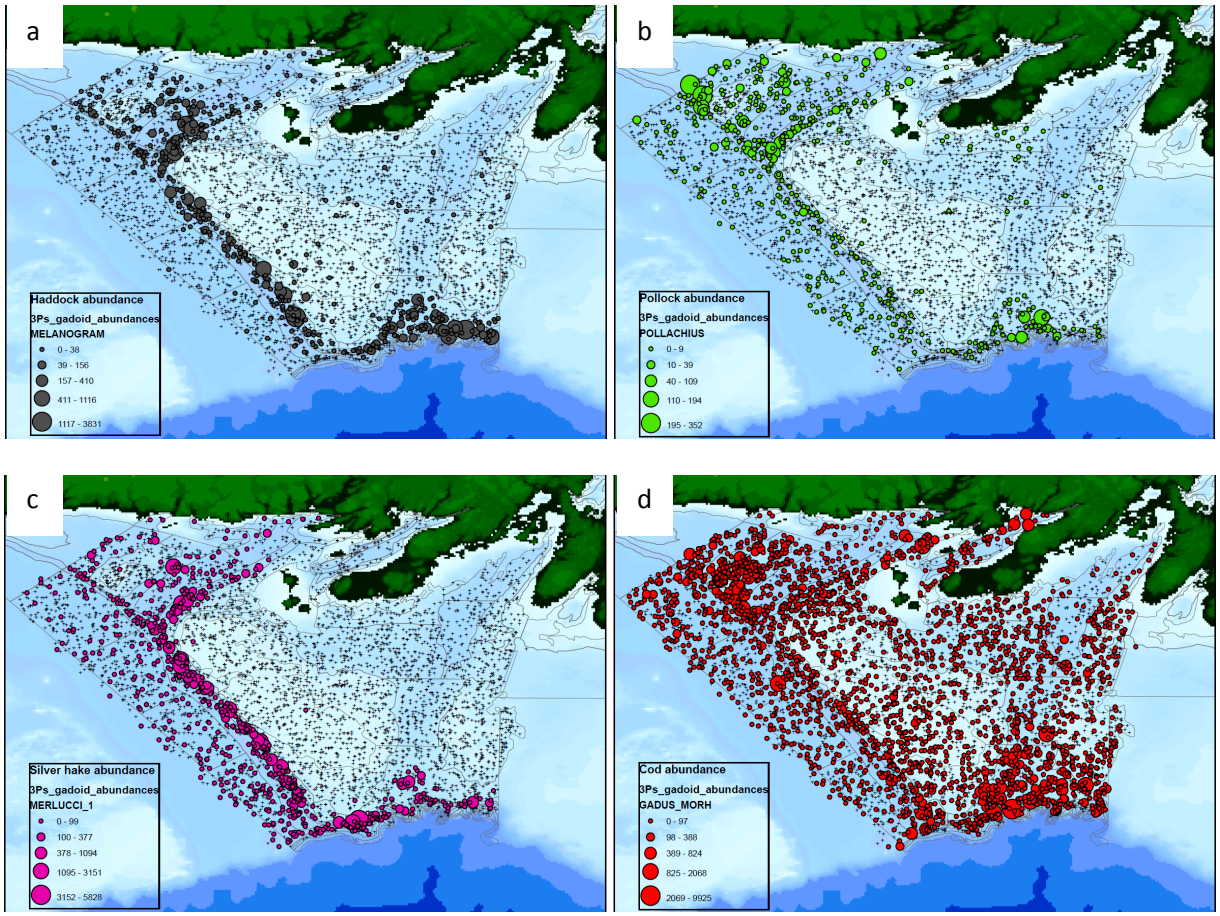

Figure 1.4a-d: Abundances of four gadoid species in 3Ps from DFO spring survey data (1993-2012). Circle diameters correspond to numbers per tow, with different scales per species. a: haddock, b: pollock, c: silver hake, and d: Atlantic cod (modified from Fisher and Koen-Alonso 2013).

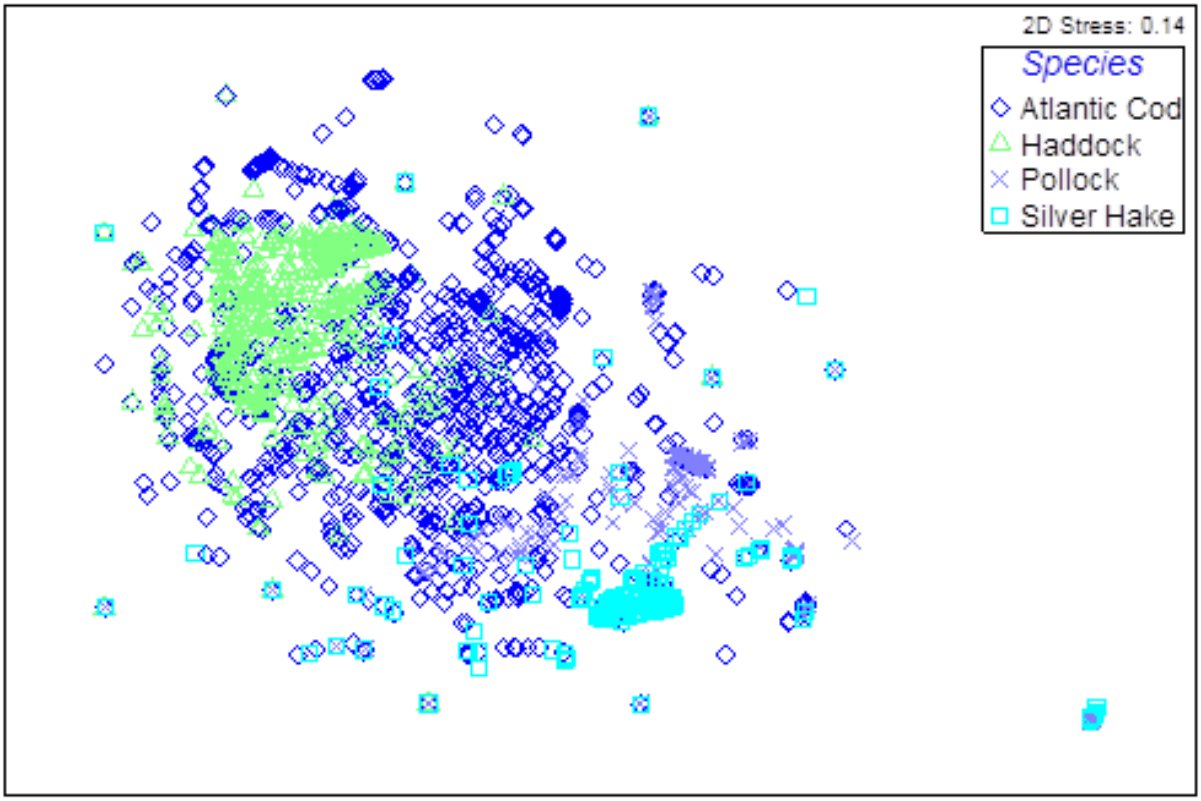

Figure 1.5: Two-dimensional non-metric multidimensional scaling ordination plot depicting diet similarity among four gadoid species (different symbols) where relative distance is proportional to the degree of diet similarity (based on the Bray-Curtis similarities between all pairs of stomachs sampled in Subdivision 3Ps).

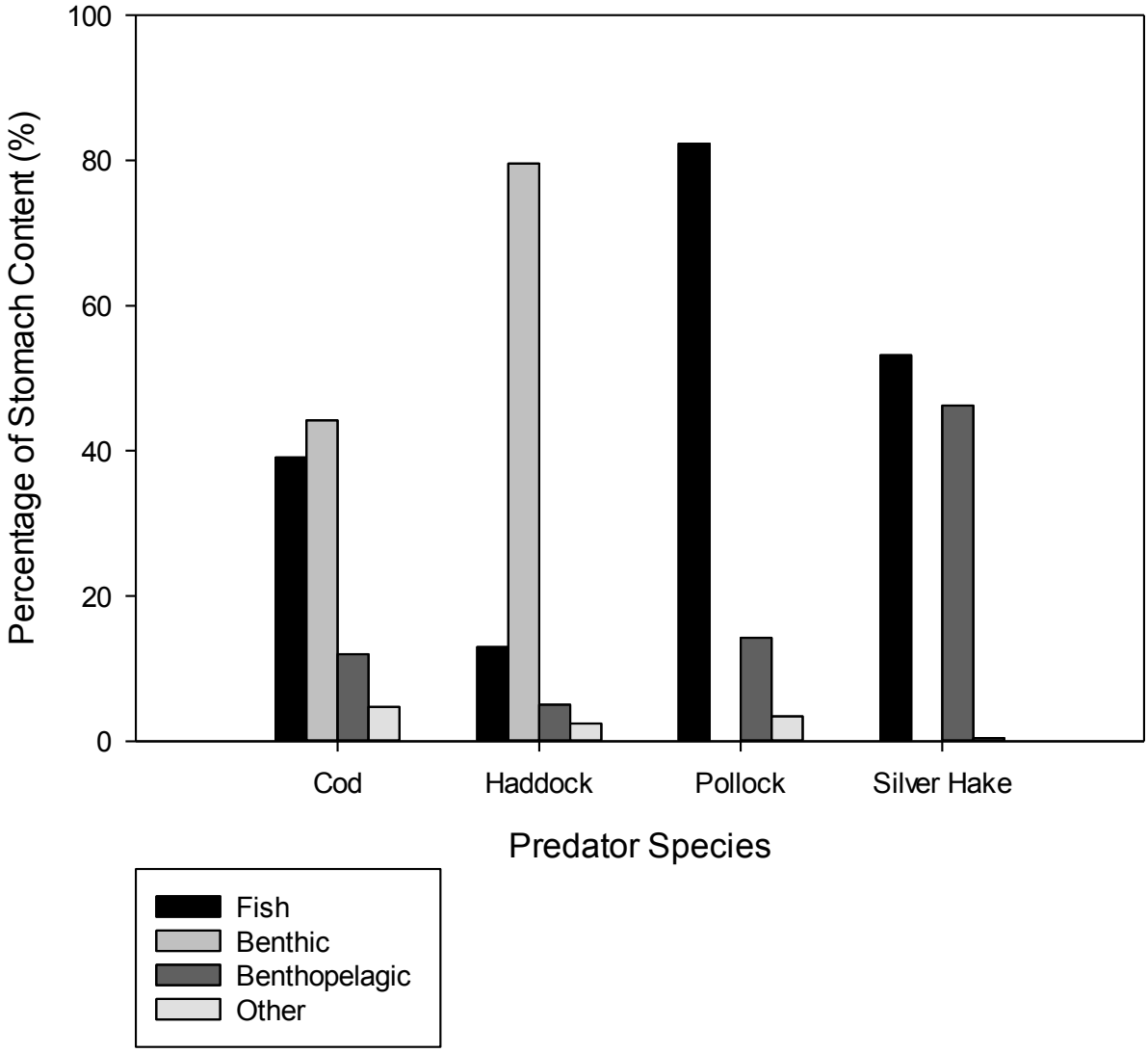

Figure 1.6: Diets of four gadoid species over three years characterized by stomach contents within four broad prey groups.

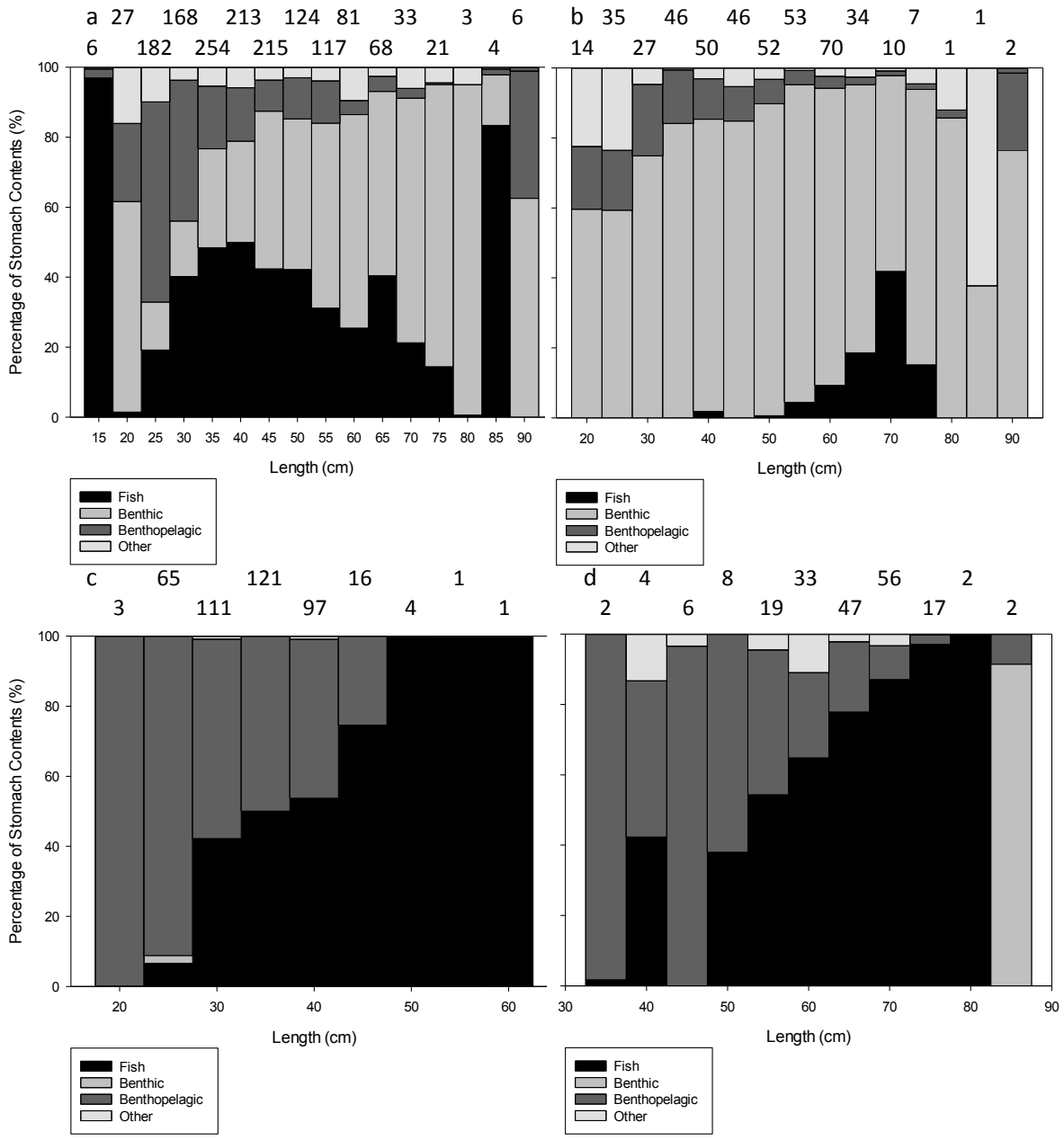

Figure 1.7a-d: Diets of four gadoid species within 5 centimeter length classes. Numbers above each bar represent the sample size for each length. a: Atlantic cod, b: haddock, c: silver hake, and d: pollock.

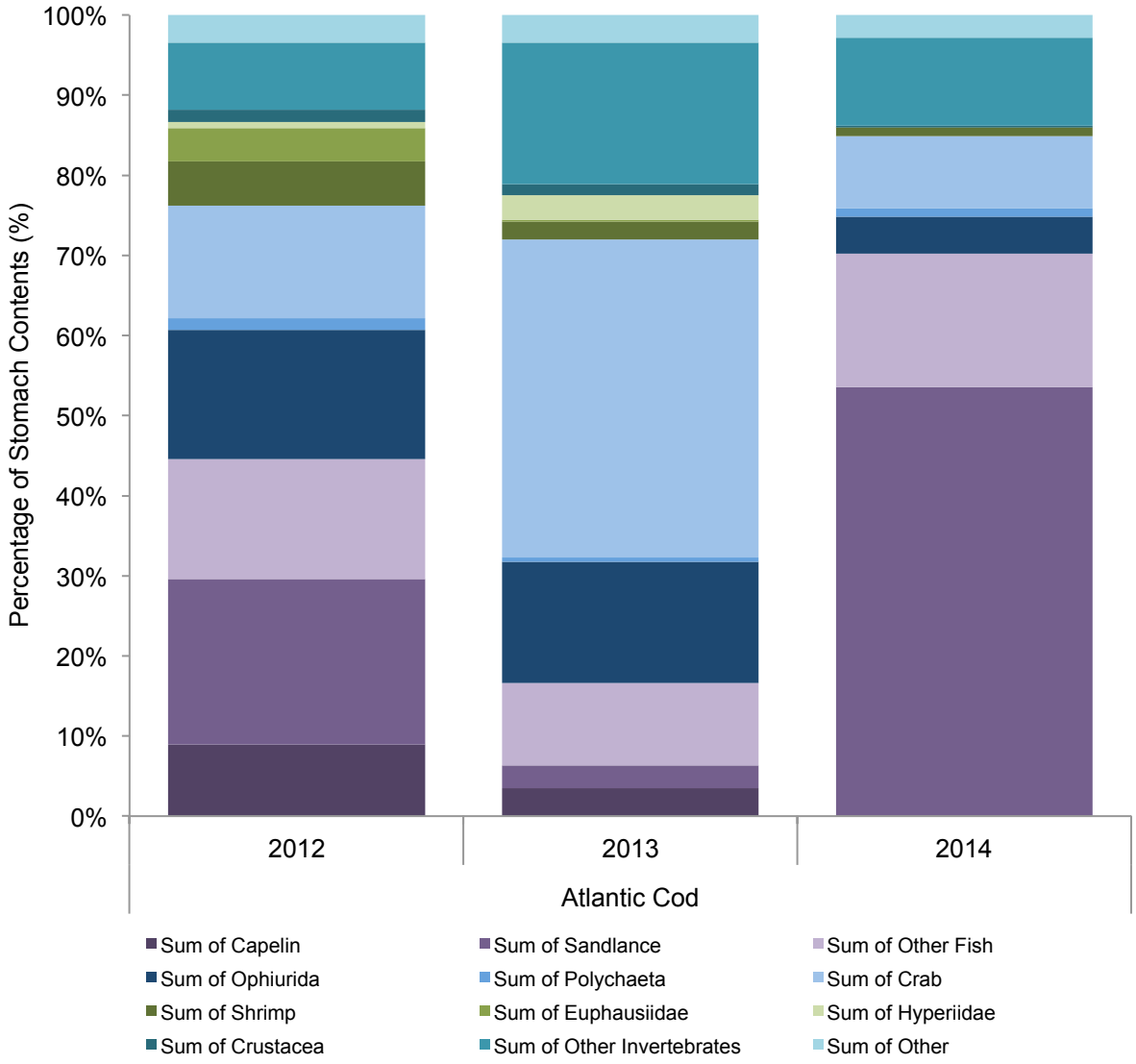

Figure 1.8: Atlantic cod diet across three years (n = 1522). Most dominant prey types by wet weight were sandlance (2012 & 2014) and crabs (2013).

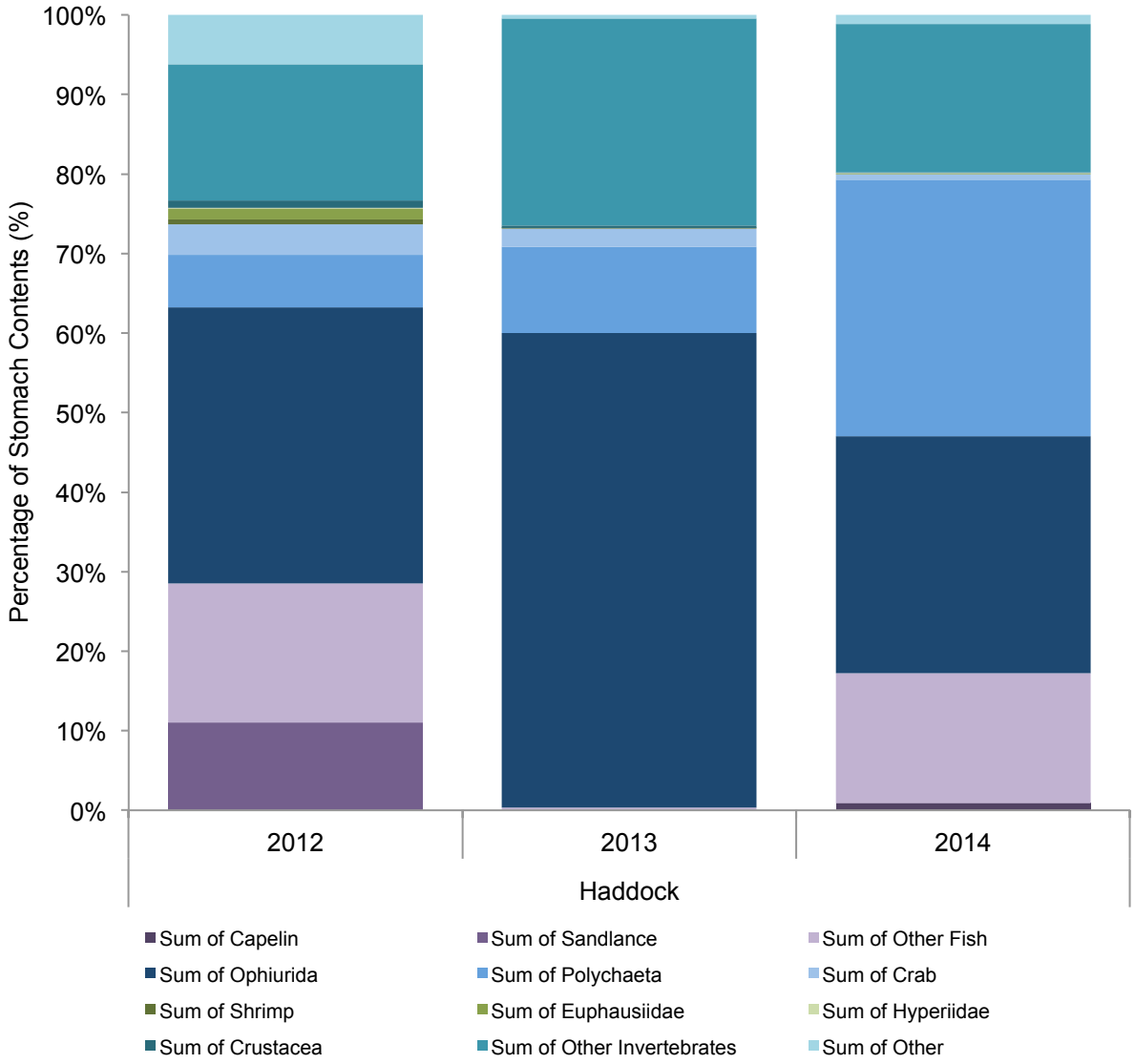

Figure 1.9: Haddock diet across three years (n = 448). Most dominant prey types by wet weight were brittle stars (2012 & 2013) and polychaete worms (2014).

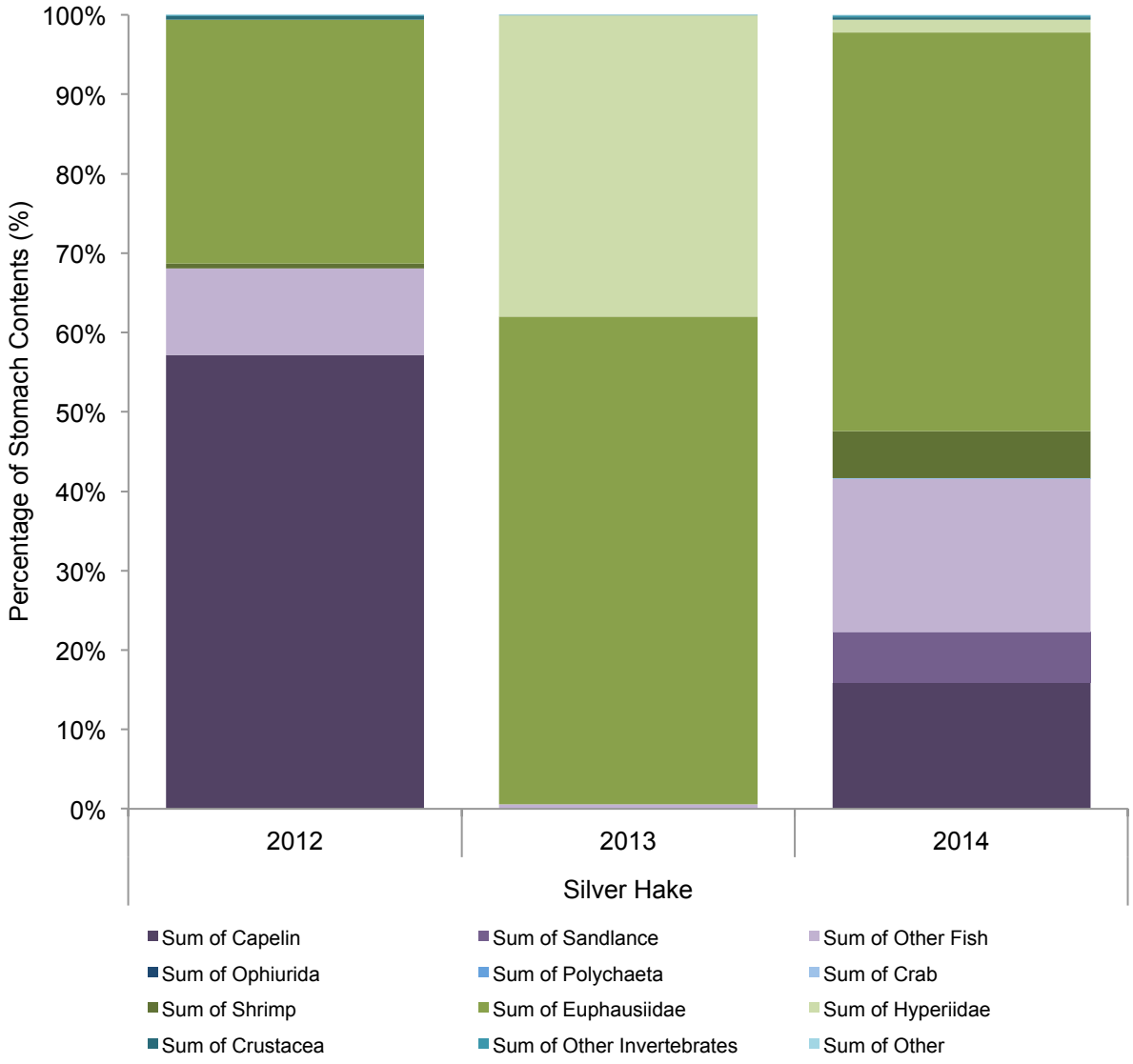

Figure 1.10: Silver hake diet across three years (n = 419). Most dominant prey types by wet weight were capelin (2012) and euphausiids (2013 & 2014).

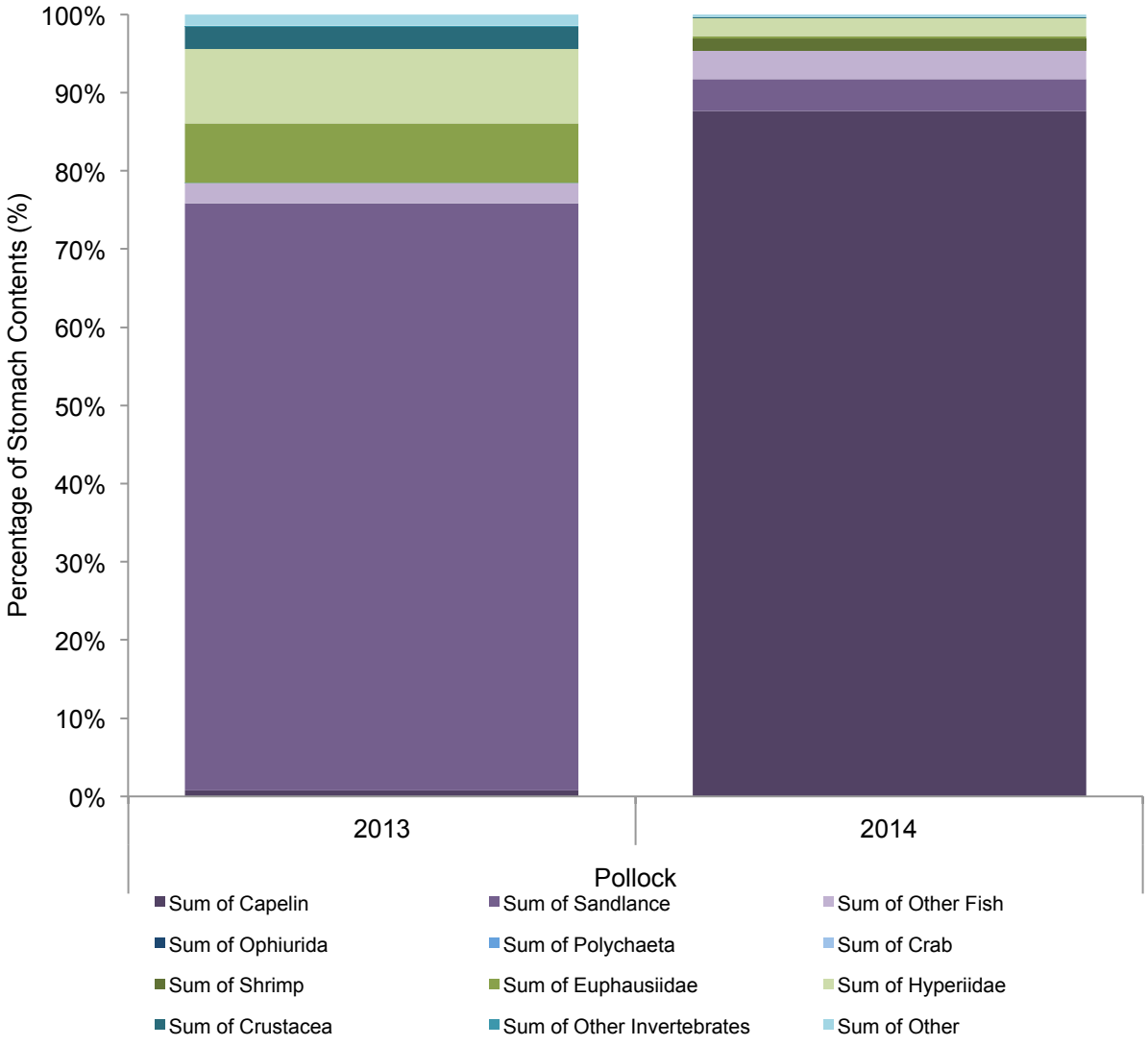

Figure 1.11: Pollock diet across two years (n = 196). Most dominant prey types by wet weight were sandlance (2013) and capelin (2014).

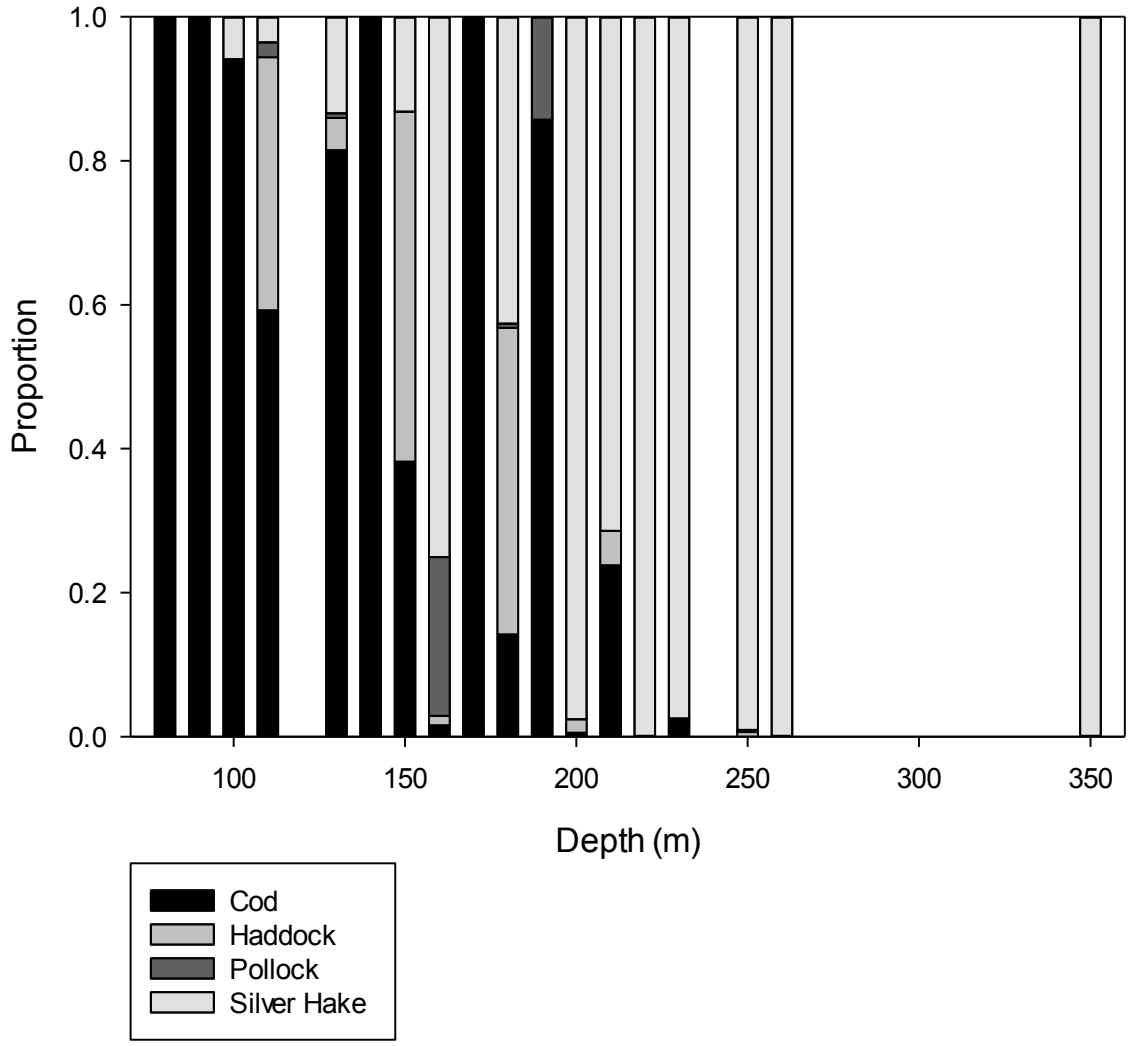

Figure 1.12: Proportional abundances by depth from the 2014 CFER survey to illustrate the depth stratification of species in the water column, which may influence measures of dietary overlap. Proportions were calculated from the number of fish caught at each depth.

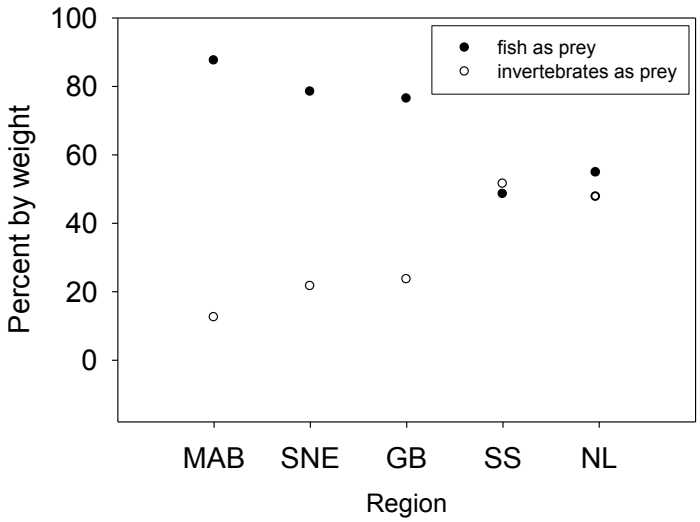

Figure 1.13: Silver hake consumption of fish and invertebrate prey by region. Data for the Mid-Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB), and Scotian Shelf (SS) are from Helser et al. (1995), while data from the current study (NL) are added for comparison.

Chapter 2. Range and abundance shifts of gadoid species in Southern Newfoundland waters under changing ocean conditions

2.1 Abstract

Shifts in spatial and depth distributions in response to warming marine waters can lead to changes in community composition and colonization and extinction on local to regional scales. Quantifying distributional shifts provides insight into species interactions, population management, and conservation. Northwest Atlantic Fisheries Organization (NAFO) Subdivision 3Ps is a faunal transition zone containing the northern range limits of a number of gadoid species including haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), and silver hake (*Merluccius bilinearis*). Recent decadal-scale increases in spring bottom water temperatures could lead to shifts in these species' spatial distributions or increased abundances at their northern range extents. Using data collected by both Fisheries and Oceans Canada on surveys from 1996-2012 and by the Centre for Fisheries Ecosystems Research in 2012 and 2014**,** changes in spatial distributions over time were analyzed by calculating changes in abundance, biomass, and the proportion of occupied sets; maximum and minimum latitude of occurrence; and design-weighted mean latitude, depth, and temperature of abundance. Atlantic cod (*Gadus morhua*) was increasingly found in cooler, shallower waters, and the mean temperature of haddock abundance also decreased over time; there were no significant distributional shifts for pollock, but silver hake shifted northward and increased in abundance, biomass, and areal extent. The recent incursion of silver hake has led to increased spatial overlap with Atlantic cod.

2.2 Introduction

Depending on habitat availability, mobile marine species tend to shift their distributions latitudinally and/or to different depths to stay within the bounds of thermally optimal habitat (e.g. Taylor et al. 1957, Frank et al. 1990, Murawski 1993, Pörtner 2002, Drinkwater 2005, Barange and Perry 2009, Chen et al. 2011, Perry 2011, Hare et al. 2012, Sunday et al. 2012, Nye et al. 2014). Oceanic warming may lead to the introduction and persistence of species that favour warmer temperatures, leading to possible changes in abundances, predator-prey overlap, spatial distributions, and associated range expansions and contractions (Cushing 1974, Murawski 1993, Winder and Schindler 2004, Schweiger et al. 2008, Nye et al. 2009, Kempf et al. 2010, Sunday et al. 2012). This has potential implications for resident species, including those targeted by commercial fisheries. However, a significant increase in populations of 'southern' species and/or previously abundant fishes may lead to the establishment of new commercially beneficial fisheries (Baudron and Fernandes 2014, Shackell et al. 2014). One of the most challenging aspects of fisheries management is trying to understand the responses of living marine resources to contemporary changes in ocean temperature. Therefore, it is important for fisheries ecologists to study this relationship to understand the stocks. As species shift their distributions in three-dimensional space in response to changes in their environment, an increased understanding of these dynamics will identify where populations of fish species are growing and shrinking.

There are certain thermal thresholds in which species can operate metabolically and perform biologically necessary enzyme-catalyzed biochemical processes and reactions (Gillooly et al. 2001). Temperatures at which physiological functioning is ideal fall within an optimal thermal threshold (Brett 1956, Fry 1958). Some species have narrow thresholds, while others' are broad, but these are not always static (Pörtner 2002) and can be defined by both evolutionary

and contemporary processes and stresses (Allen et al. 2006). Optimal thermal ranges can change based on metabolic activity, with some species spawning in warm waters, but feeding in colder ones; and with age and size (Gillooly et al. 2001), as with species that hatch in warmer waters and move into cooler waters as adults or vice versa. The thermal ranges species are able to inhabit often largely dictate their distribution on a wide spatial scale (Drinkwater 2005, Rose 2005a, Tittensor et al. 2010). Distributional patterns of some fish species reflect their relative sensitivities to water temperatures to some extent (Murawski 1993). For species that have been found to closely track thermal regimes, it can be possible to predict range expansions, contractions, and shifts using oceanographic data (Nye et al. 2011, Sunday et al. 2012).

With increased demands from government, industry, and the public for more information about ecosystem changes related to climate change, research targeting new information on the distributions and interactions among gadoids is necessary (Shackell et al. 2014, Stortini et al. 2015). The goal of this study was to investigate the current spatial, depth, and temperature distributions of four gadoid species in springtime southern Newfoundland waters in relation to climate change and global climate cycles and compare the results to those from earlier studies in adjacent areas (Almeida 1984, Nye et al. 2009, Nye et al. 2014, Stortini et al. 2015). The species of interest were haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), silver hake (*Merluccius bilinearis*), and Atlantic cod (*Gadus morhua*). Warming ocean temperatures may be the cause of increased abundances of non-cod gadoids in 3Ps, and if population structure, community assemblages, and biogeography are changing, species interactions are undoubtedly changing as well (Tylianakis et al. 2008).

If conditions in southern Newfoundland waters are becoming thermally more similar to those on the neighbouring Scotian Shelf, there is a possibility that the ecosystem will need to be

managed and utilized in novel ways to remain sustainable (Link et al. 2011). Spatial distribution data can be used to gain a better understanding of the stocks (Ulltang 1996, Link et al. 2011, Shackell et al. 2014, Stortini et al. 2015), information that will be crucial in the potential development of a monitoring index or even opening a silver hake fishery in 3Ps.

It was hypothesized that the observed increases in bottom temperature would illicit one or more of the following responses: an expansion (southern species) or contraction (northern/resident species) of spatial range, an increase in mean latitude of abundance, or a change in mean depth and/or temperature of abundance. However, while Atlantic cod has a widespread distribution on the slope as well as on the cooler banks (Figure 1.3d), the non-cod gadoids examined are considered south-temperate bank, slope, and basin species (Scott 1982, Almeida 1984, Helser et al. 1995, Mahon et al. 1998, Lock and Packer 2004, Fisher and Koen-Alonso 2013, DFO 2015b, Stortini et al. 2015). Therefore, at the northern extent of their ranges, they are predominantly found on the outer edges of the shelf and on the shelf slope in spring (Figures 1.3a-d) when hydrographic conditions on the shallow banks are too cold and therefore less suitable (Templeman and Hodder 1965, Murawski 1993). Because of this spatial distinction, it was expected that the most informative metrics would be depth and temperature. Additionally, it was hypothesized that distributional shifts would be associated with changes in abundance, biomass, or both.

2.3 Methods

2.3.1 Study Area

NAFO Subdivision 3Ps borders the south coast of the island of Newfoundland and contains Burgeo, St. Pierre, and most of Green Bank. On two sides it is bordered by Hermitage

and Laurentian channels and also contains Halibut channel. As a result of its location and complex bottom topography, there exist complex temperature gradients and suitable hydrographic conditions for species that inhabit cooler, shallower habitat and those found in warmer, deeper waters (Colbourne and Murphy 2005, Colbourne et al. 2013, Colbourne et al. 2014). This area is a thermal transition zone and contains the northern range endpoints of some gadoid and some non-gadoid fish species (Pinhorn and Halliday 1997).

2.3.2 Field Sampling

The Centre for Fisheries Ecosystems Research (CFER) carried out an acoustic transect survey with acoustic-directed bottom trawl fishing sets in spring 2012-2014 aboard the Research Vessel *Celtic Explorer*. This vessel used a scientific echo sounder (Simrad EK60 at frequencies of 18, 38, 120, 200 kHz) to direct fishing sets toward 'gadoid' signal on echograms as identified by experts and with reference to prior gadoid signal (mostly Atlantic cod) (e.g. Rose 1992, Rose 1993, Knickle and Rose 2012). Using gadoid signal as a director of fishing location, a total of 26 fishing sets were completed in 2012, 8 in 2013, and 27 in 2014, largely targeting the shelf slope region (Figure 1.3). Set locations were spread over a range of depths on the shelf and shelf slope. In 2012 and 2014, a Campelen 1800 shrimp trawl was used (Walsh and McCallum 1997) and in 2013 a Grand Overture Verticale (GOV) trawl (ICES 2012) was used. To maintain consistency of analyses, four inshore sets from 2012 were omitted to focus on the same areas that characterize 'core strata' (Figure 1.2b, described below) from the DFO surveys and all sets from 2013 were omitted due to the gear change. The date, time of day, duration, location, depth, and bottom temperature of fishing sets were recorded (Table A.1).

Upon the completion of a set, all net contents were separated and species were identified and weighed. In the surveys from 2012 and 2014, 1868 Atlantic cod, 1003 haddock, 399 pollock, and 6135 silver hake were caught (Table A.2). The majority of sampling was on the shelf slope (exclusively so in 2014 due to survey design), which was dictated by the presence of gadoid acoustic signal (Figure 1.3). This pattern corresponded with data collected by DFO on the spatial distributions of these four gadoid species: that in spring, their distributions overlap largely along the edges of the shelf and on the shelf slope and only Atlantic cod is found in large abundances in shallow shelf waters (Figures 1.4a-d). In all three years, survey fishing effort was concentrated on shelf slope locations where gadoid signal was present and fishing set locations were largely based on what was detected by the echo sounders.

Fisheries and Oceans Canada has conducted bottom trawl surveys for the purpose of research since 1972 (DFO 2014a, DFO 2015a) within a 'core area'. In 1997, more inshore areas were added to the survey design, increasing its area by 12% (Figure 1.2b, Figure 2.1). For the purpose of this study, only the core strata were used in analyses. The survey has been conducted every year, but in 2006 was not fully completed (DFO 2014a). Data from 2006 were omitted for this reason. Annual stock assessments use these survey data because the survey is designed to reflect overall ecosystem trends, timed to assess resident species, and standardized over the majority of the ecosystem area (DFO 2015a). The survey area was stratified by depth ranges and fishing sets were randomly assigned within each depth stratum (Doubleday 1980). The majority of abundance and biomass of my target species was often found in only a few strata in spring. These strata have typically been located where Halibut Channel and Laurentian Channel meet, around 45°N (Figure 1.2b, Figure 1.4a-d, Figure 2.1). The catch from each 15 minute trawl was

counted and weighed and the trawl area was extrapolated to the stratum area. From this, the extrapolations were combined to estimate total biomass and abundance (DFO 2015a).

This study predominantly used abundance data within the 'core area' exclusively from surveys carried out from 1996-2012, as these are the years in which the survey was conducted in April and May using a Campelen 1800 shrimp trawl (Table 2.1). Within this subset of years and locations, there were 2383 sets completed with 1682 sets containing Atlantic cod, 201 with haddock, 190 containing pollock, and 433 with silver hake. In total, 1827 sets contained at least one of the four species of interest, about 77% of the total number of sets. Given that there are two years of data from the CFER surveys that were usable for this study, these were compared to the DFO survey results and these targeted sets were used to examine the most recent characteristics of gadoid distributions in southern Newfoundland waters in the spring. The data from both surveys used in this study overlapped in 2012, abundance indices in this year were compared between surveys using a two-tailed t-test comparing latitude, depth, and temperature bins.

2.3.3 Analyses of Spatial Metrics

Survey design-weighted fish distribution data for Atlantic cod, haddock, pollock and silver hake were analyzed over time from 1996-2012 using the DFO survey data. Raw gadoid abundance data from each set were combined using a weighting strategy that incorporated strata area data so that the subpopulations sampled in each stratum were combined appropriately (based on stratum area weightings) to represent the population as a whole (Cochran 1977, Perry and Smith 1994). In these analyses, measures of abundance were used while sex and size/age

were not taken into account. Overall patterns could be observed without these measurements although their omission decreases the precision of the conclusions drawn (Murawski 1993).

To investigate the relationship between shifts in spatial distributions and changing ocean conditions, a number of distributional parameters were considered that have been used to characterize temporal change within other systems (e.g. Dulvy et al. 2008, Nye et al. 2009, Nye et al. 2011, Pinsky et al. 2013). These included the maximum and minimum latitude, depth, and temperature of occurrence, and weighted mean latitude, depth, and temperature of abundance. Additionally, changes in the overall abundance of four species and biomass of haddock, pollock, and silver hake were quantified, while range expansions and contractions were estimated through the percentage of sets occupied by each species over time (Fisher and Frank 2004, Liow and Stenseth 2007). First, design-weighted mean abundances per tow were calculated for each year and species as described in Cochran (1977), using the equation:

$$y_{st} = \frac{\sum_{h=1}^{L} N_h y_h}{N}$$

Where y_{st} is the mean stratum-weighted abundance, N_h is the area of stratum h, y_h is the abundance from the i^{th} tow in stratum h, and N is the total area of all L strata in a given year. Abundance-weighted mean spatial parameters were calculated as described in Nye et al. (2009), using the equation:

$$X = \frac{\sum_{i=1}^{n} w_i X_i}{\sum w_i}$$

Where X represented the abundance-weighted overall mean of the parameter of interest (latitude, depth, or temperature), X_i was the parameter in set i, and w_i was log (design-weighted abundance + 1) of each species for each set i.

After the weighted means of spatial metrics were calculated, general linear models relating the calculated values over time were used to explore significant distributional shifts over the course of the survey. Non-cod gadoid biomass data and total abundances were regressed over time to calculate potential statistically significant changes. While no single-parameter model could explain all the variation in the data, a linear regression was found to be the most appropriate option out of several analyses that were explored. In the case of depths and temperatures, abundance data were plotted against design-weighted depth and temperature data as per Perry and Smith (1994), and a two tailed t-test was used to determine if the abundance was statistically different from the sampled depths and temperatures. In order to examine temporal autocorrelation and ensure independence of the response variable, its residuals were plotted against the residuals lagged by one time interval (Schabenberger and Pierce 2001, Brockwell and Davis 2006, Zuur et al. 2010). In cases where the data did not meet the assumptions of the general linear model, transformations were used to ensure the data being analyzed were independently, identically, and normally distributed. When analyzing proportional data, which by definition cannot be normally distributed, a logit transformation was applied to these data as detailed in Warton and Hui (2011).

Using mean number per tow data that were transformed to presence-absence data, the degree of overlap between all pairs of species was calculated for each pair of species, overall, and by year. For pairwise tests of positive association a 2 x 2 table (Table 2.2) and Chi-square test was used, as detailed in Cole (1949). Overall, the proportion of sets that contained both species was calculated for all pairs of species. These proportions were calculated overall, by dividing the number of instances of co-occurrence by the total number of sets including at least one of the four study species. Next, the data were separated by year, underwent a logit-

transformation, and the degree of spatial overlap indexed by this method was regressed over time to investigate whether co-occurrence changed over time. Furthermore, interspecific diet similarity percentages were plotted against spatial overlap percentages (see also Chapter 1) to investigate if there was a statistically significant relationship between the two. If two species were from the same functional group and co-occurred in space, this could increase the diet overlap and potential for competitive interactions and intraguild predation.

2.4 Results

2.4.1 Latitude

In 2012 and 2014 on the CFER surveys, Atlantic cod was caught at almost all latitudes sampled. Haddock was most frequently collected at lower latitudes with one exception in 2012. In 2012, pollock was only caught at latitudes above 47°N, but in 2014 almost all of the pollock was caught in one set at 44.928°N. Silver hake, like cod, was found at a wide range of latitudes, but had a lower mean latitude of abundance (Figure 2.2a, Figure 2.3, Table 2.3). The DFO data provided a more comprehensive view of latitudinal distribution, but many of the same patterns were observed (Figure 2.2b, Figure 2.3, Figures 2.4a-d, Table 2.4).

Based on the DFO survey time series, a change in the mean latitude of abundance over time was significant for silver hake (Figure 2.4c-d, $p = 0.021$) which had an average annual increase of 0.0298°N. This equates to an approximate average northward shift of about 3.3 kilometers per year. A change in the maximum latitude of occurrence was significant only for cod ($p = 0.004$) and occurred at an average rate of 0.9 kilometers southward per year, while minimum latitudes of occurrence over time did not significantly change for any of the four species (Table 2.4, Table 2.5, $p > 0.25$).

2.4.2 Depth

In the CFER surveys from 2012 and 2014, Atlantic cod had the shallowest mean depth of abundance, was present in almost all sets down to 257 meters, and was the only species caught in depths shallower than 95 meters. Haddock and pollock had similar and narrower depth distributions. Silver hake had a wider depth range, comparable to Atlantic cod, but on average was found in deeper waters, up to 346 meters (Figure 2.5a, Figure 2.6, Table 2.3). The DFO survey sampled a greater range of depths, but the data generally presented similar patterns as the targeted CFER data. Atlantic cod was the most abundant species at both the shallowest (less than 200 meters) and deepest (more than 300 meters) depths, while silver hake was the dominant catch species from 200 to 290 meters. At depths in excess of 550 meters, cod and silver hake were the most abundant species in certain sets. Haddock and pollock had patchier depth distributions, and did not compose the majority of the catch at any depth (Figure 2.5b, Figure 2.6, Figures 2.7a-d, Table 2.4).

As shown in Figure 2.7a, a change in the mean depth of design-weighted abundance over time was significant only for cod ($p = 0.014$), which decreased an average of 4.8 meters per year from 1996 to 2012. Conversely, the maximum and minimum depths of occurrence over time did not change significantly for any species (Table 2.4, Table 2.5, $p > 0.06$). When abundance was compared to design-weighted sampled depths, the two were found to be significantly different for all species ($p > 0.44$).

2.4.3 Temperature

From the CFER surveys in 2012 and 2014, cod was caught in the widest range of temperatures, between -0.6°C and 8.7°C, and had the lowest mean temperature of abundance.

The acoustic signature of Atlantic cod was targeted for this survey, so habitat where this signal was detected was most frequently sampled. The CFER survey covered a subset of the area surveyed by DFO, and both surveys found Atlantic cod inhabited the widest temperature range of the four species (Figure 2.9). As with depth, haddock and pollock had similar, narrower temperature ranges, and the same mean temperature of abundance (4.8°C). Silver hake had the warmest mean temperature of abundance, with the vast majority of hake being caught in temperatures above 6°C (Figure 2.8a, Figure 2.9, Table 2.3). The catches from the DFO surveys showed cod as being present at almost all temperatures between -1.4°C and 9.5°C, with the lowest mean temperature of abundance. The non-cod gadoids all had mean temperatures of abundance between 5 and 6°C. Haddock and pollock occupied similar temperature ranges. Silver hake was caught in the narrowest range of temperatures and had the highest mean temperature of abundance (Figure 2.8b, Figure 2.9, Figures 2.10a-d, Table 2.4).

Mean temperature of design-weighted abundance over time exhibited a significant change for cod ($p = 0.001$) which decreased at an average annual rate of 0.08°C and haddock ($p = 0.009$) with an average annual decrease of 0.11°C (Figure 2.10a-b). Maximum temperature of occurrence over time significantly changed only for silver hake (Figure 2.10d, $p = 0.049$) which increased at an average rate of 0.08°C per year from 1996-2012. A change in minimum temperature of occurrence over time was not significant for any of the four species (Table 2.5, $p > 0.28$). When abundance was compared to design-weighted sampled temperature, the two were found to be significantly different for all species ($p > 0.4$). Temperature and depth were analyzed with respect to one another and were found to be positively correlated to Atlantic cod abundance. Haddock abundance did not experience the same relationship.

2.4.4 Spatial Range, Abundance, Biomass, and Spatial Overlap

Only silver hake showed a significant increase in the percentage of occupied sets over time (Figure 2.11, $p = 0.008$). The percentage of sets containing silver hake nearly quadrupled between 1996 and 2012. While there was significant variation in the data, the overall trend observed and quantified was that the design-weighted average abundance per tow of silver hake showed a significant increase over the time series (Figure 2.12, Table 2.5, $p = 0.033$). On average, more than 580 additional fish were caught per year from 1996 to 2012. Additionally, silver hake biomass increased significantly over time (Figure 2.13, $p = 0.006$), and large catches of silver hake were only encountered in years with higher mean annual temperatures. When the residuals of spatial metric analyses were tested for spatial and temporal autocorrelation, it was found there was no significant autocorrelation among the data. There appeared to be a strong relationship between distribution and abundance, especially for silver hake. When this relationship was quantified, it was found that there was a significant positive relationship between the percentage of occupied sets and the design-weighted mean abundance per tow for haddock, pollock and silver hake (Figure A.3).

From the DFO data, it was calculated that all pairs of gadoids had positive associations, except for cod and haddock. When measuring co-occurrence, cod and silver hake had the highest incidence of co-occurrence at 17.57%, 10.24% of sets contained cod and haddock, with cod and pollock co-occurring in 9.25%, haddock and silver hake in 4.98%, haddock and pollock in 3.28%, and pollock and silver hake in 5.04% of sets. 1.59% of sets contained all four species. When the logit –transformed data were regressed over time, none of the pairs had a statistically significant increase or decrease in co-occurrence throughout the time series. However, cod and silver hake were the closest to showing a statistically significant positive relationship over time

(Figure 2.14, p = 0.066). As discussed above, haddock and pollock had very similar depth and temperature ranges (Figure 2.6, Figure 2.9); however, this pair had the smallest overlap percentage as a result of small catch abundances and patchy distributions (Table 2.1). The degree of spatial overlap was compared to the degree of diet similarity for all pairs of species (Figure 2.15). While the relationship was not statistically significant, the two were positively correlated, meaning a lack of co-occurrence may be one of the drivers of low interspecific diet overlap (see Chapter 1). There was one year of overlap between the CFER and DFO surveys. When abundance indices from this year were compared between surveys, it showed that although they showed similar patterns of latitudinal, depth, and temperature distribution, they were statistically different. This is most likely due to the small number of sets over a limited spatial extent in the CFER survey.

2.5 Discussion and Conclusions

Measured increases in bottom temperatures in NAFO Subdivision 3Ps were expected to initiate responses in the ecosystem particularly related to changes in biogeography (Drinkwater 2005, Rose 2005a). While shifts in distribution can be dependent on habitat availability and complexity, the predicted responses in this study were increases in mean latitude of abundance, changes in mean depth and temperature of abundance; spatial range expansions of warmer water species and/or contractions of resident, cooler water species; and changes in overall abundances, biomass, or both. It was also hypothesized that due to differences in the habitat preferences or occurrences of the study species, depth and temperature would be the most informative metrics.

The results of this study clearly showed that there were significant biogeographical changes occurring in warming southern Newfoundland waters over the time series. The most

prominent shifts were seen in silver hake that exhibited statistically significant increases in areal extent, abundance, biomass, maximum temperature of occurrence, and mean latitude of abundance between 1996 and 2012. It is notable that these changes occurred outside of the closest stock management area (NAFO 4VWX) and that no Newfoundland survey data sources have been incorporated into assessment advice (Stone et al. 2013). Fall surveys may be useful in determining whether the 3Ps population is distinct or mixes with the adjacent Scotian Shelf stock.

2.5.1 Latitude

Originally, it was hypothesized that because cod inhabits both shallow shelf habitat and warmer shelf slopes and channels while non-cod gadoids mainly inhabit the warmer waters of the slopes and channels (Taylor et al. 1957, Mahon et al. 1998), that latitude would be a less informative spatial metric compared to depth and temperature in 3Ps, due to the complex bottom topography and temperature gradients in the region. However the mean latitude of abundance of pollock and silver hake significantly increased over time, despite the physical characteristics of the region. For these species, shifts in latitude are a well-documented response to warming (e.g. Taylor et al. 1957, Frank et al. 1990, Murawski 1993, Barange and Perry 2009); therefore it was a result supported by other studies. Because the depth and temperature distributions of these species did not exhibit a significant change, this species likely continued to inhabit the shelf slope, but shifted northward along the edge of the shelf.

The maximum latitude of occurrence of cod decreased over the time series, while the minimum latitude of occurrence did not change significantly. This aligned with the hypothesis that resident, cooler water species would exhibit a range contraction (Nye et al. 2009), although

the proportion of occupied sets did not significantly change over time for this species. Therefore, it cannot be concluded with a great amount of certainty that this observation indicated that there was a reduction in the range of cod. In addition, it is important to consider the available habitat as well as the oceanographic conditions of the sampled habitats compared to the habitats where a species of interest was found, which is why design-weighted abundances were used in analyses.

2.5.2 Depth

Expected shifts in cod abundance in response to warming were observed in the form of significant shifts to shallower waters that are cooler in spring. This was consistent with findings from other climate change-distribution response studies (Nye et al. 2009). What was not consistent with prior studies was the magnitude of depth shift. For example, Dulvy et al. (2008) found that many species exhibited changes in depth of abundance in the North Sea, with most species deepening within the range of 0.6 to 14 meters per decade. This range falls well below the more than 48 meter per decade shift in mean Atlantic cod abundance that was calculated from the DFO data. Reasons for this result are not fully understood, and highlight 3Ps as a unique ecosystem that is experiencing changes and species responses that differ from adjacent regions. More detailed analyses are recommended, as outlined below.

One issue that arose was from limitations of using size- and age-aggregated abundance data. Without information regarding size or age composition of the catch, we were not able to conclude definitively whether changes in cod distribution were the result of an overall shift to shallower waters, or a fishing effect. Smaller, younger fish tend to occur more frequently in shallower waters, while larger, more mature fish are found at deeper depths (Kao and Fletcher 1988). If, as a result of the fishery removing large cod from the population, the survey was

catching larger quantities of younger, smaller cod, it could lead to this result, and this finding may be driven by recent recruitment patterns exhibited by this population (DFO 2015a).

Aside from fishing mortality, other hypotheses include recruitment pulses and poor survival of older, larger individuals due to other abiotic and biotic stressors. Other analyses by DFO support both of these (DFO 2014a, DFO 2015a). Extraordinarily large year classes of Atlantic cod in 2011 and 2012 (DFO 2015a) support the recruitment theory. In recent years, the total mortality rates, which include mortality due to fishing and all other causes, of cod have been much higher than the time series average (DFO 2015a). Because less than half of the total allowable catch has been reported as landed, these rates appear to be indicative of some other cause of mortality. These rates are analyzed for fish aged 5-10 (DFO 2015a), which could support the hypothesis of poor survival of older year classes, leading to an increase in the quantity of younger fish being collected in the survey. Analysis of catch biomass, length, and age data over time would be necessary to reject the possibility of a fishing versus an environmental effect and provide more insight into the size and age structure of the catch, and by extension, the stock. However length frequency data are not collected for all species of interest in all years examined, even within the widespread DFO research survey. If this information was available, we could determine more conclusively whether and which components of the cod population are moving into shallower depths.

2.5.3 Temperature

Another anticipated distributional shift observed was a decrease in the mean temperature of occurrence of cod because a change in mean temperature of abundance often corresponds to a shift in latitude (Nye et al. 2009). However, in the present study, this was not observed. As

mentioned above, Atlantic cod were found increasingly frequently in shallower sets, which may explain the significant decrease in mean temperature of occurrence. Like with depth, biomass and length/age data would be better indicators of the structure of the stock (Saint-Germain et al. 2007), and it could not be concluded with confidence whether a cooler average temperature of abundance was due to an overall shift of the population, or a result of increased catches of younger fish, which are found in cooler waters (Kao and Fletcher 1988).

The mean temperature of haddock abundance also decreased significantly over the time series, the reasons for this are not fully understood, but may be due to increased food availability of benthic prey. Another suggestion from the literature is that density-dependent mechanisms may be the explanation (Landa et al. 2014), but in this survey, the distribution of haddock is quite patchy, so it is unlikely that this is the reason. From the linear regression models of the data being analyzed, we were unable to confirm or deny the driver of this particular shift in abundance.

The maximum temperature of occurrence of silver hake increased over the course of the survey. Because of the anomalous increases in bottom temperatures in the region, there is more warm water habitat available. Of the four species of interest, silver hake is most abundant at and most strongly associated with the warmest water temperatures (Scott 1982), so it would be expected that this species would expand into the warmest waters of 3Ps, and an increase in maximum temperature of occurrence would be observed. Because of the strong relationship between silver hake distribution and temperature, increasing bottom temperatures in this region may lead to the establishment of this species (Cormon et al. 2014).

2.5.4 Spatial Range, Abundance, Biomass, and Spatial Overlap

Changes in the frequency of occurrence in survey sets were used to approximate spatial range expansions and contractions (Fisher and Frank 2004, Liow and Stenseth 2007). Dispersion and range size can also be dictated by environmental conditions; for example, in warm years silver hake tend to be more dispersed (Cook, personal communication). As a significant increase in the percentage of sets with silver hake was measured over time, it was concluded that its range was expanding. Paired with an increase in its mean latitude of abundance, and no change in its minimum latitude of occurrence, it was determined that this species was expanding northward and increased in abundance at the northern extent of its range. As hypothesized, this was associated with an overall increase in silver hake abundance and biomass over time. However, the variance in silver hake abundance over time was very large.

All species pairs were found to be positively associated over the time series, with the exception of cod and haddock, although this pair had the second highest overlap percentage. This percentage can be considered the association index of the two species, but gives no information regarding whether this association is due to a strong interaction between the species or if it is random. In order to investigate whether spatial overlap was increasing over time, the proportion of sets in which each pair of species was calculated over all years, and for each year in order to quantify any significant trends. Overall, the species that had the largest degree of spatial overlap were cod and silver hake, and while no pairs of species exhibited a statistically significant change in overlap over time, this pair of species was close ($p \approx 0.0657$). This may be due to cod's overall large proportion of occupied sets, coupled with silver hake's emergence in 3Ps. Cod was caught in more than 60% of the total sets in all years, and over 90% of sets containing at least one of the four species of interest, and silver hake was the second most frequently

occurring, occurring over 23% of gadoid-occupied sets. Haddock and pollock were caught in about 10% of these sets.

One would expect that as spatial overlap increased, diet overlap would also increase due to prey availability and predator-prey overlap (Cushing 1974, Winder and Schindler 2004, Schweiger et al. 2008, Kempf et al. 2010). This association was quantified, and there was a positive relationship, but it was not statistically significant. This tells us that you can't infer one from the other, so it is important to study both aspects in order to have a comprehensive understanding of trophic interactions and competition among species that have overlapping spatial distributions (Figure 2.15).

On the CFER surveys, we found that silver hake preyed heavily upon capelin in some years (see also Chapter 1), which could lead to competitive interactions between silver hake and larger cod that tend to consume more finfish prey. However, more than 75% of sets that contained cod did not contain silver hake. For this reason, among others detailed in Chapter 1, this most likely would not have negative implications for cod at this time of year, but the emergence of hake has been seen to exert significant pressure on gadoids in other ecosystems (e.g. Temming et al. 2007, Baudron and Fernandes 2014, Cormon et al. 2014).

In recent years, an increase in non-cod piscivorous gadoid biomass in NAFO Subdivision 3Ps caused Atlantic cod to no longer the dominant member of this functional group in this region in the spring. Increases in the abundance of silver hake caught in research trawls have garnered interest in regards to this species' growing role in the ecosystem in southern Newfoundland waters (DFO 2015a), and its roles as predator, competitor, and commercially exploitable species. Currently, there is no stock assessment for this species in 3Ps, and data from Newfoundland

waters are not included in stock assessments for adjacent stocks (DFO 2015b). Link et al. (2011) detail the importance of including distributional shifts into management considerations.

On the northeast United States continental shelf, silver hake is among the most mobile piscivorous species (Lock and Packer 2004). Silver hake occupies a relatively narrow optimal thermal range, and has been found to move in space in order to stay within this range (Murawski and Finn 1988). On the Scotian Shelf in 2014, silver hake reached its highest biomass since the 1980s (DFO 2015b) and exhibited a positive relationship between local abundance and geographic distribution (Fisher and Frank 2004). Increasing silver hake abundance at the northern extent of its range is largely due to its mobile nature and tendency to track thermal conditions as more favourable temperatures develop in 3Ps.

While cod was increasingly caught in cooler, shallower waters, silver hake had the most dramatic distributional shifts in all dimensions between 1996 and 2012. It was shown that there was an increase in silver hake abundance and biomass, in addition to an expansion of its spatial range associated with an increase in the frequency of occurrence in fishing sets and a northward shift in its mean latitude of abundance. From year to year, catches varied significantly, but large catches and biomass were only observed at higher temperatures. Therefore if warming continues and conditions become more like those farther south as they are predicted, the same distributional trends can be expected to persist. As a result, assemblages in this region may continue to change and an altered management plan that includes consideration of data from Newfoundland waters in stock assessments of silver hake if more data becomes available.

Data from the 3Ps side of the Laurentian Channel should be used in assessments of adjacent stocks. Also, much can be learned from expanding surveys to different times of year to

investigate whether silver hake in southern Newfoundland waters are moving between NAFO areas. If this is the case, the spring survey would simply be a double count of a stock that may inhabit different management areas during other times. This would also provide more insight on seasonal differences in spatial and depth distributions, as these are currently unknown. With novel findings of significant changes in distributions and increases in abundance, biomass, and range extent, it is crucial that we continue to study and monitor the changes this ecosystem is experiencing, in order to best understand the effects of climate change on regions containing biogeographical boundaries.

As bottom water temperature increases, mobile marine species tend to shift poleward or change their depth distributions in the majority of studies (e.g. Frank et al. 1990, Murawski 1993, Pörtner 2002, Rahel 2002, Walther et al. 2002, Drinkwater 2005, Perry et al. 2005, Barange and Perry 2009, Chen et al. 2011, Last et al. 2011, Perry 2011, Hare et al. 2012, Nye et al. 2014). With measured warming in southern Newfoundland waters, quantifying changes in biogeography can provide data on potential changes in predator-prey and more general species interactions. Moreover, when the spatial distributions of some species shift, it may lead to novel competitive interactions for spawning and nursery grounds, as well as other spatial resources. This study was developed due to increases in the catches of non-cod gadoids in 3Ps, the need felt by researchers to quantify these increases, and the subsequent interest in how these species were affecting resident species and the characteristics of their spatial distributions in the region.

Table 2.1: Total catches (kg) of four gadoid species in southern Newfoundland waters by DFO in 1996-2012.

Year	Mean Depth (m)	Mean Temperature (◦C)	Cod	Haddock	Pollock	Silver Hake
1996	206.7133	2.5551	3249.85	31.133	17.489	163.667
1997	200.875	2.1472	1093.92	8.81	8.778	5942.111
1998	196.3253	2.57	9409.88	252.651	200	1041.822
1999	218.3403	2.942	2548.49	667.946	136.818	571.84
2000	199.0629	3.0333	2957.85	779.556	10.032	1230.26
2001	204.2797	2.2413	5380.13	263.333	322.222	2775.46
2002	202.4521	2.4178	4090.42	312	6.889	467.222
2003	203.5103	1.7944	3655.3	74.667	92.889	578.667
2004	197.6327	2.4582	2890.31	253.683	59.578	532.067
2005	211.0188	3.1429	5975.94	163.47	19.738	87.924
2006						
2007	197.7619	1.9241	2606.41	3878.6	21.778	842.911
2008	200.2409	2.3276	2521.1	46.571	10.921	3279.111
2009	200.9861	2.6902	4501.14	110.8	35.222	1182.556
2010	198.1918	2.875	5398.2	252.098	248.552	12589.251
2011	198.7517	3.3103	3300.29	132.095	16.143	19011.771
2012	199.9726	3.0897	4638.94	229	272.667	8048.397

Table 2.2: Testing the association between pairs of gadoid species using all sets from all years with the exception of 2006.

Atlantic cod and silver hake			
	silver hake present	silver hake absent	
Atlantic cod present	321	1384	1705
Atlantic cod absent	112	10	122
	433	1394	1827
Pollock and silver hake			
	silver hake present	silver hake absent	
pollock present	92	101	202
pollock absent	341	1293	1625
	433	1394	1827
Haddock and silver hake			
	silver hake present	silver hake absent	
haddock present	91	111	202
haddock absent	342	1283	1625
	433	1394	1827
Atlantic cod and haddock			
	haddock present	haddock absent	
Atlantic cod present	187	1518	1705
Atlantic cod absent	15	107	122
	202	1625	1827
Atlantic cod and pollock			
	pollock present	pollock absent	
Atlantic cod present	169	1536	1705
Atlantic cod absent	24	98	122
	193	1634	1827
Haddock and pollock			
	pollock present	pollock absent	
haddock present	60	142	202
haddock absent	133	1492	1625
	193	1634	1827

Table 2.3: Distributional parameters for four gadoid species based on biomass using CFER data 2012/14. 1868 Atlantic cod, 1003 haddock, 399 pollock, and 6135 silver hake

Species	Mean Abundance (Δabund/yr)	Mean Proportion of Sets Occupied (Δprop./yr)	Poleward Movement (km/yr)	Mean Latitude (°lat/yr)	Maximum Latitude (°lat/yr)	Minimum Latitude (°lat/yr)	Mean Depth (m)	Mean Temp (◦C)
Cod	934 (-666) p = 0.068	80.42 (-15.035) p = 0.117	-38.5	45.665 (-0.3461)	47.4 (-0.4948)	44.9051 (-0.047)	141.58	3.55
Haddock	501.5 (149.5) p = 0.736	38.112 (-7.343) p = 0.886	-35.6	45.3543 (-0.3201)	46.882 (-0.4652)	44.9284 (-0.0353)	147.12	4.80
Pollock	199.5 (196.5) p = 0.314	18.007 (8.916) p = 0.632	-112.1	46.1282 (-1.0083)	47.218 (-0.6332)	44.9284 (-1.0393)	141.78	4.80
Silver Hake	3067.5 (2573.5) p = 0.034	63.112 (17.657) p = 0.273	-26.2	45.5592 (-0.2357)	47.4 (-0.625)	44.9051 (-0.047)	196.93	6.59

Table 2.4: Distributional parameters for four gadoid species based on abundance using DFO data from 1996-2012.

Species	Mean Abundance Per Tow (Δabund/yr)	Mean Proportion of Sets Occupied (Δprop./yr)	Poleward Movement (km/yr)	Mean Latitude (°lat/yr)	Maximum Latitude (°lat/yr)	Minimum Latitude (°lat/yr)	Mean Depth (m) (m/yr)	Mean Temp (◦C) (°C/yr)
Cod	22.94105	71.953	-0.3781	46.0924	47.4767	44.815	176.8662	2.6375
	(0.4328)	(0.4053)		(-0.0034)	(-0.0081)	(0.0024)	(-4.8149)	(-0.076)
	p = 0.38	p = 0.118		p = 0.465	p = 0.004	p = 0.259	p = 0.014	p = 0.001
Haddock	2.69329	8.1613	-0.4003	45.6686	47.34	44.8367	180.3171	5.192
	(0.1026)	(0.1043)		(-0.0036)	(0.0072)	(-0.0019)	(-3.0275)	(-0.1101)
	p = 0.698	p = 0.446		p = 0.787	p = 0.608	p = 0.675	p = 0.113	p = 0.009
Pollock	0.52241	8.2138	4.6704	46.2192	47.4767	44.815	220.4769	5.3703
	(0.027)	(0.1044)		(0.042)	(0.0348)	(-0.0088)	(-0.5367)	(0.0191)
	p = 0.43	p = 0.477		p = 0.198	p = 0.19	p = 0.608	p = 0.781	p = 0.673
Silver	16.88871	16.592	3.3138	45.7734	47.4567	44.81	270.7009	5.9676
Hake	(2.54)	(0.9305)		(0.0298)	(0.0025)	(0.0032)	(2.1683)	(0.0371)
	p = 0.033	p = 0.008		p = 0.021	p = 0.797	p = 0.274	p = 0.176	p = 0.244

Table 2.5: Summary of all spatial shifts of four gadoid species based on abundance data from DFO (1996-2012).

Species	Depth	Temperature	Latitude	Range	Abundance
Cod	Mean decreased	Mean decreased	Maximum decreased (~1 km/yr)	No change	No change
Haddock	No change	Mean decreased	No change	No change	No change
Pollock	No change	No change	No change	No change	No change
Silver Hake	No change	Maximum increased	Mean increased (~3 km/yr)	Increased	Increased

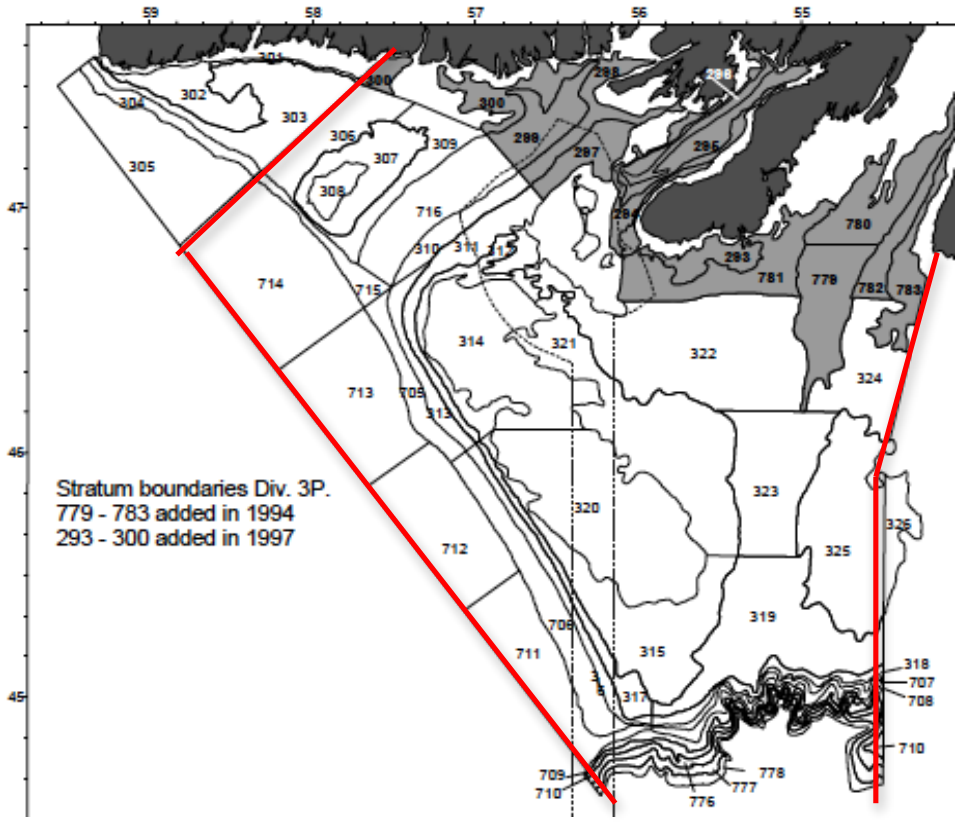

Figure 2.1: Stratum boundaries in NAFO Division 3P. 3Ps is outlined in red. The un-shaded strata represent the core strata. The dashed line represents the French economic zone, which is included in the survey (modified from Healy et al. 2010).

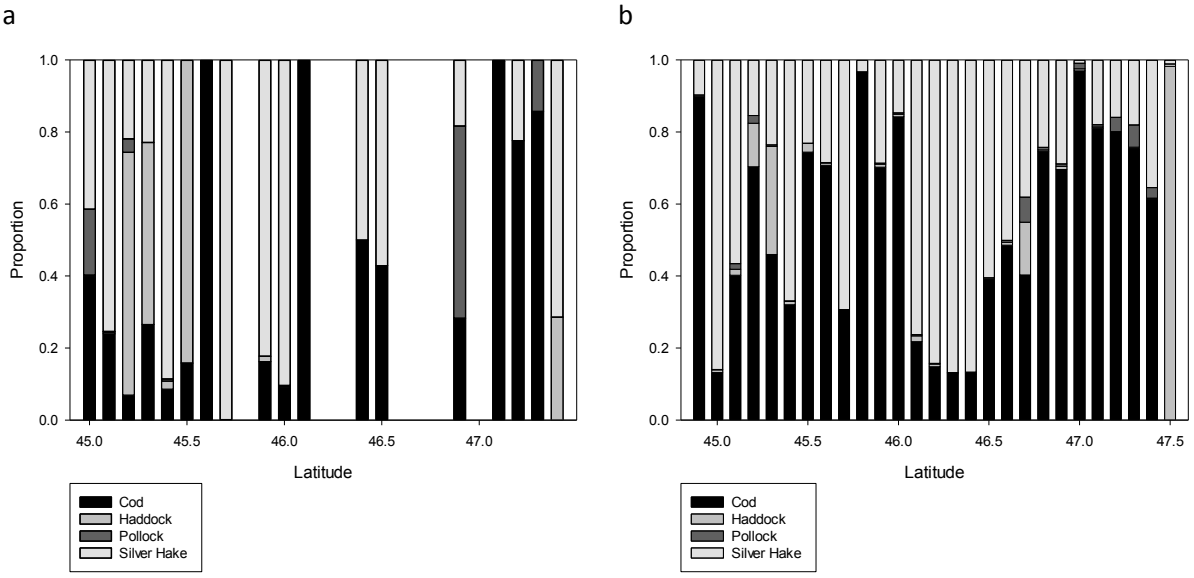

Figure 2.2a-b: Comparing the catches of four gadoid species with increasing latitude using a: CFER data from 2012 and 2014 and b: DFO data from 1996-2012.

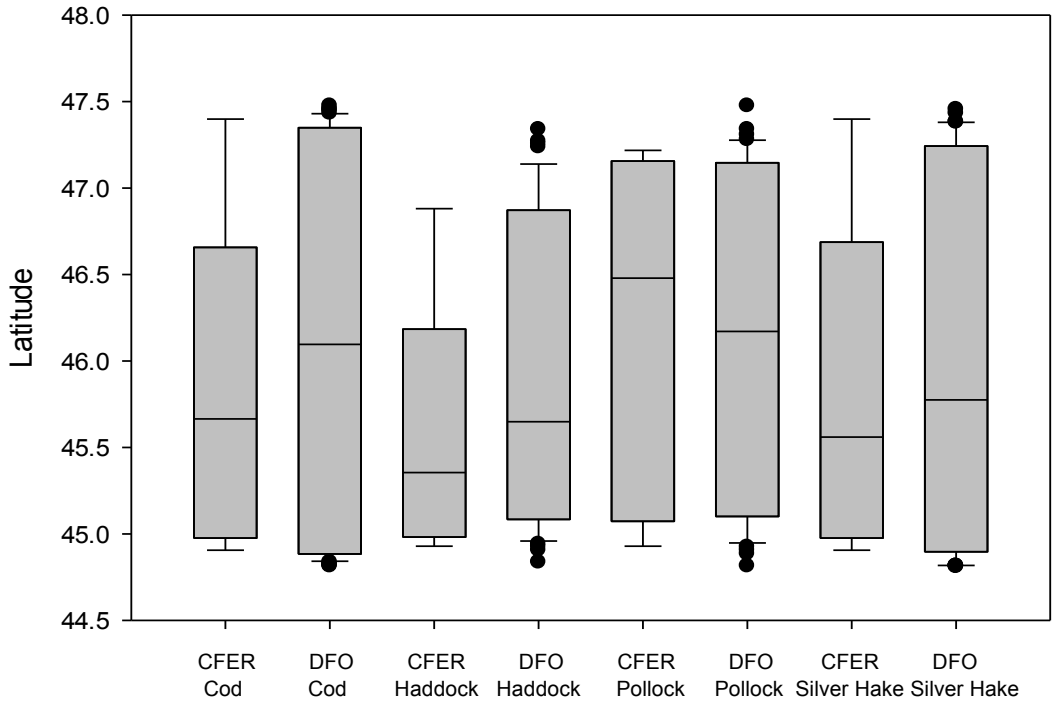

Figure 2.3: Boxplots illustrating the 25th and 75th percentiles and median weighted latitude of abundance of four gadoid species in two surveys.

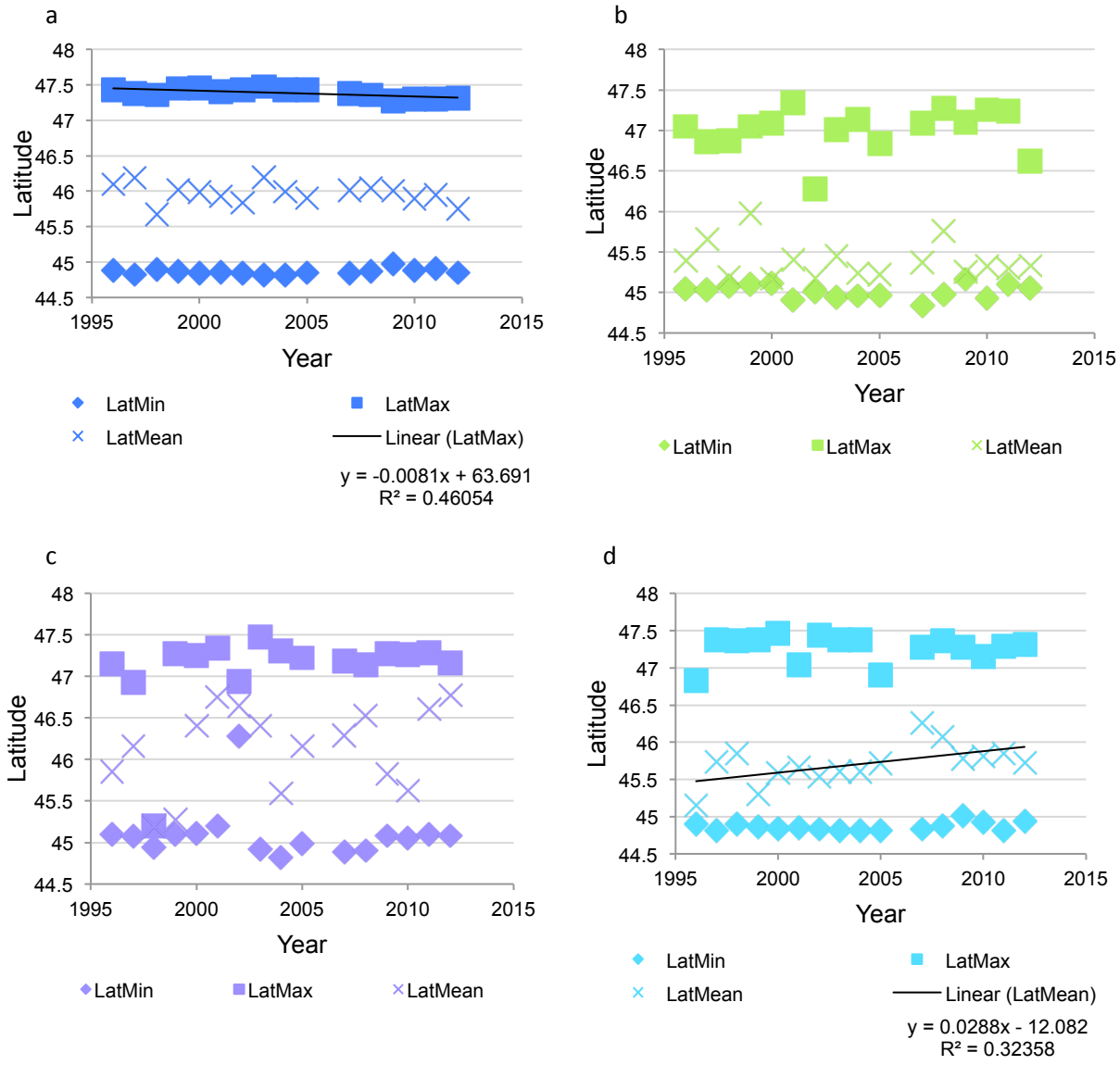

Figure 2.4a-d: Minimum and maximum latitude of occurrence and mean latitude of abundance of four gadoid species using DFO data from 1996-2012. Trend lines were calculated from linear regression models with time as the explanatory variable. a: Atlantic cod, maximum latitude of occurrence decreased significantly over time ($p < 0.05$); b: haddock, no significant latitudinal changes ($p > 0.6$); c: pollock, no significant latitudinal changes ($p > 0.19$); and d: silver hake, mean latitude of abundance increased significantly over time ($p < 0.05$).

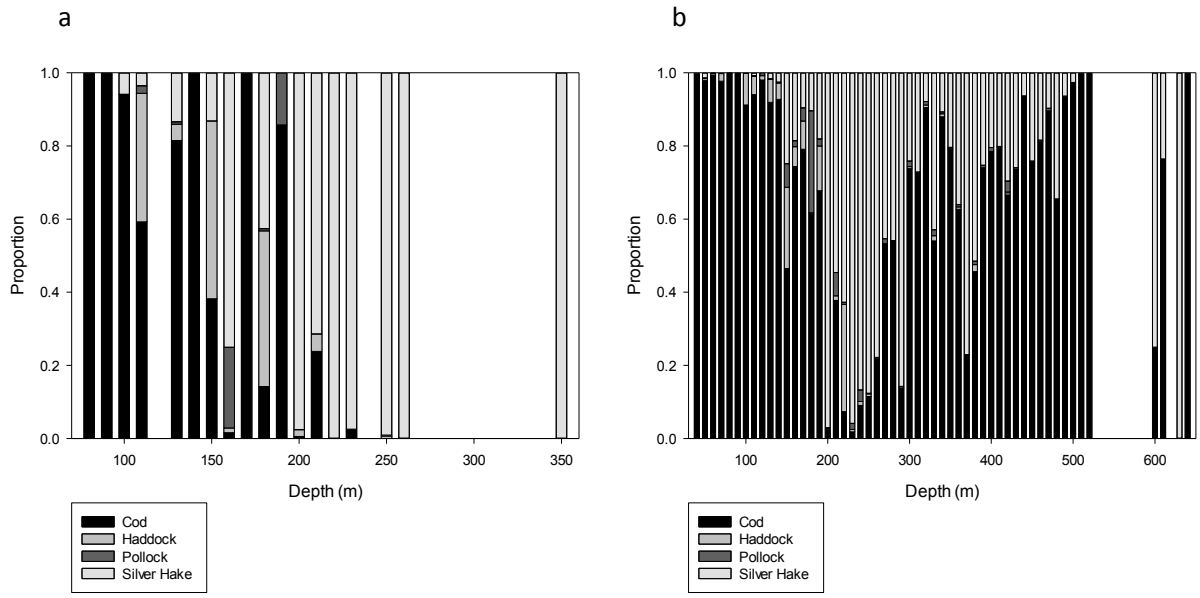

Figure 2.5a-b: Comparing the catches of four gadoid species with increasing depth using a: CFER data from 2012 and 2014 and b: DFO data from 1996-2012.

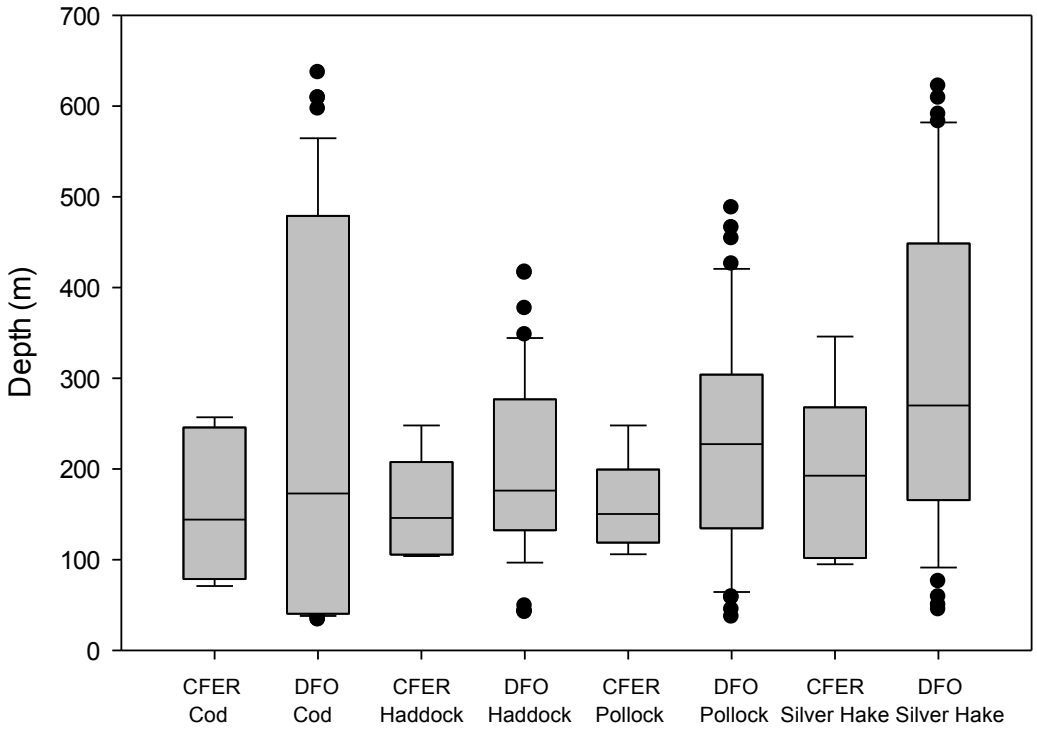

Figure 2.6: Boxplots illustrating the 25th and 75th percentiles and median weighted depth of abundance of four gadoid species in two surveys.

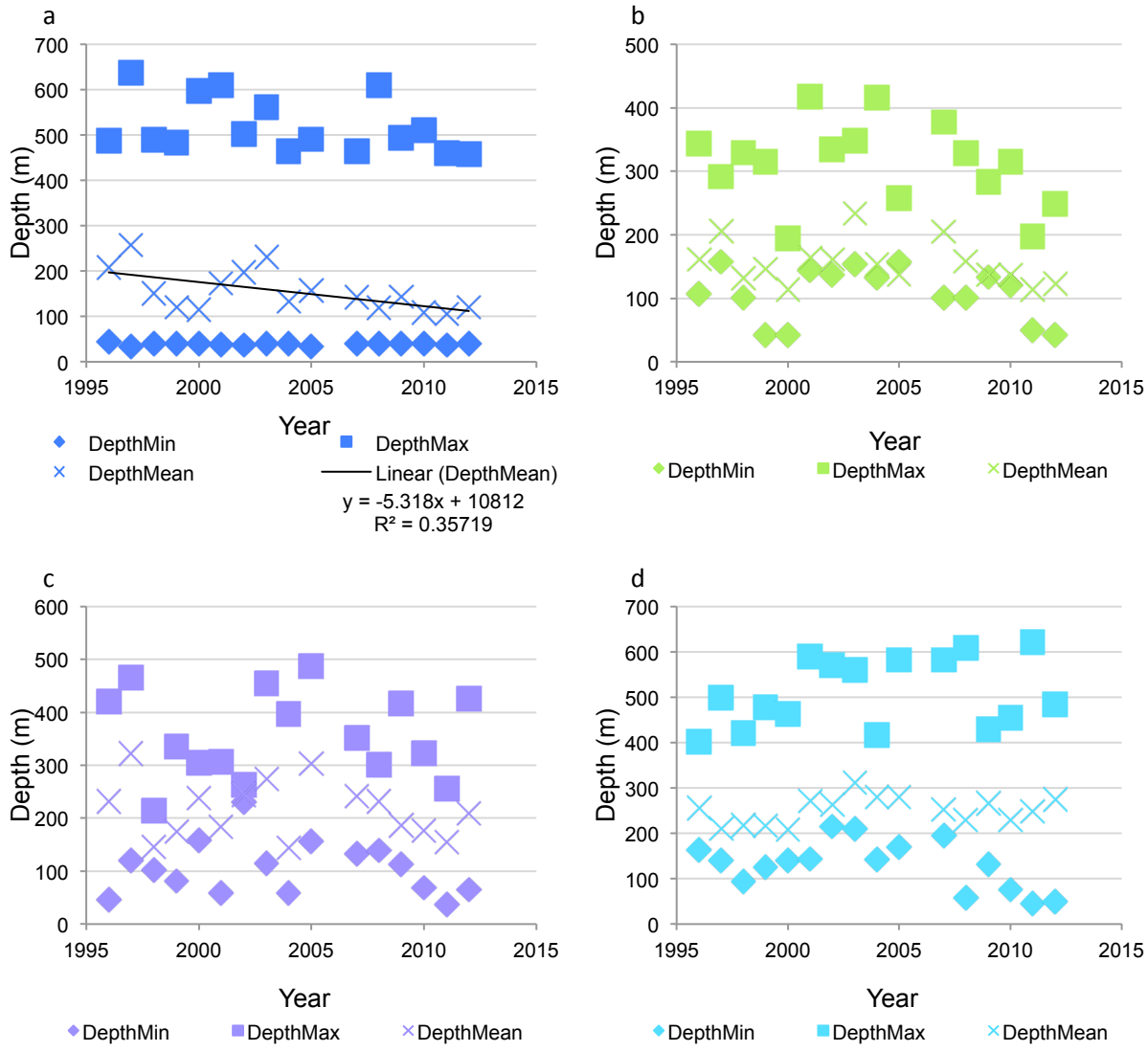

Figure 2.7a-d: Minimum and maximum depth of occurrence and mean depth of abundance using DFO data from 1996-2012. The trend line was calculated from a linear regression model with time as the explanatory variable. a: Atlantic cod, mean depth of cod abundance decreased significantly over time ($p < 0.05$); b: haddock, no significant depth changes ($p > 0.11$); c: pollock, no significant depth changes ($p > 0.63$); and d: silver hake, no significant depth changes ($p > 0.06$).

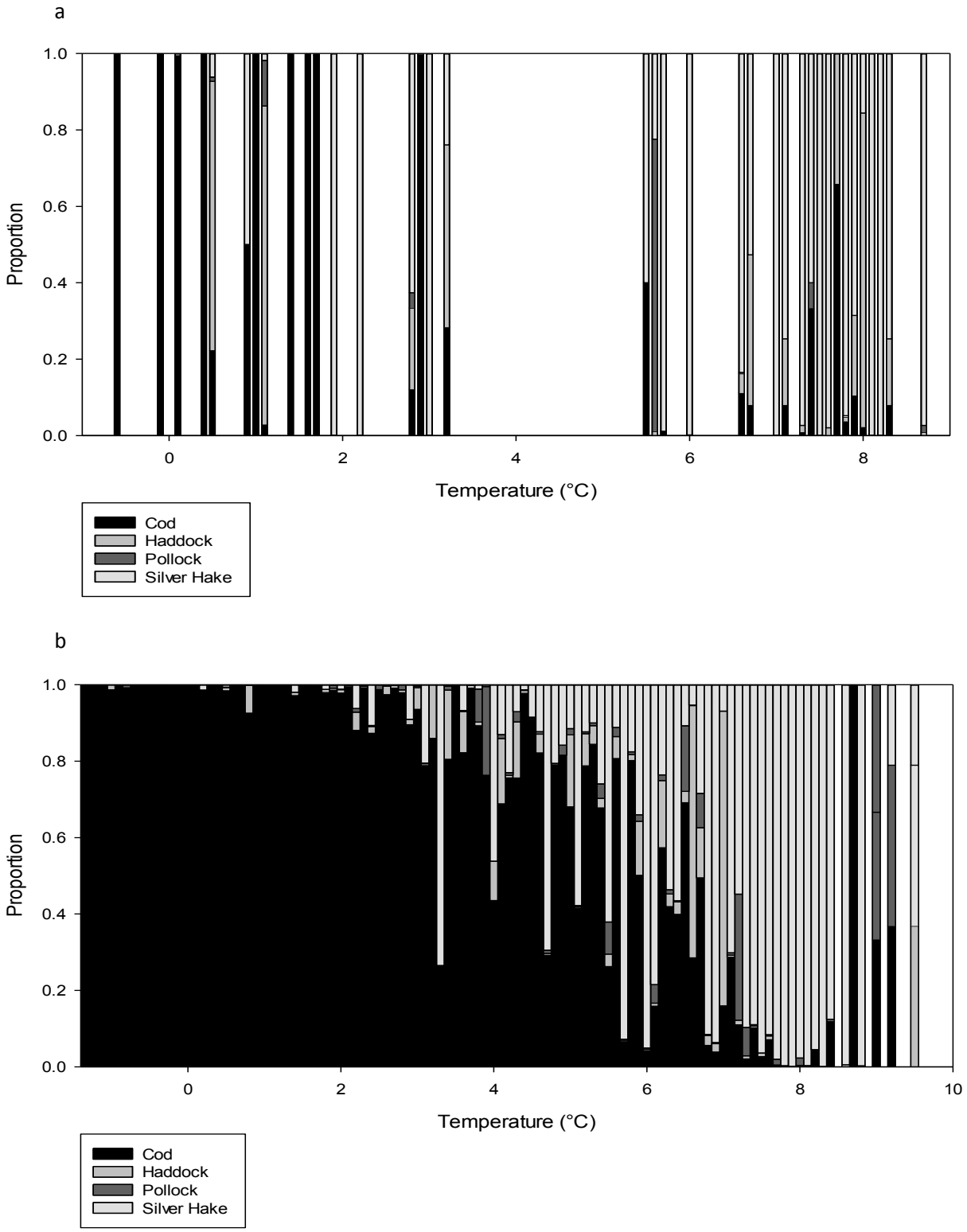

Figure 2.8a-b: Comparing the catches of four gadoid species with increasing temperature using a: CFER data from 2012 and 2014 and b: DFO data from 1996-2012.

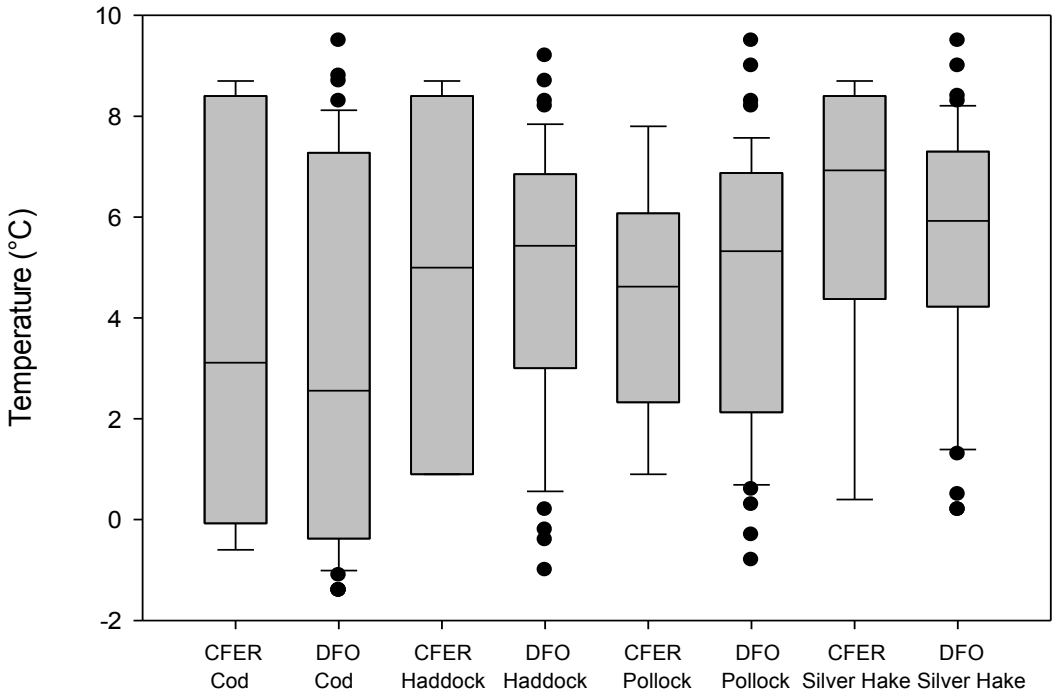

Figure 2.9: Boxplots illustrating the 25th and 75th percentiles and median weighted temperature of abundance of four gadoid species in two surveys.

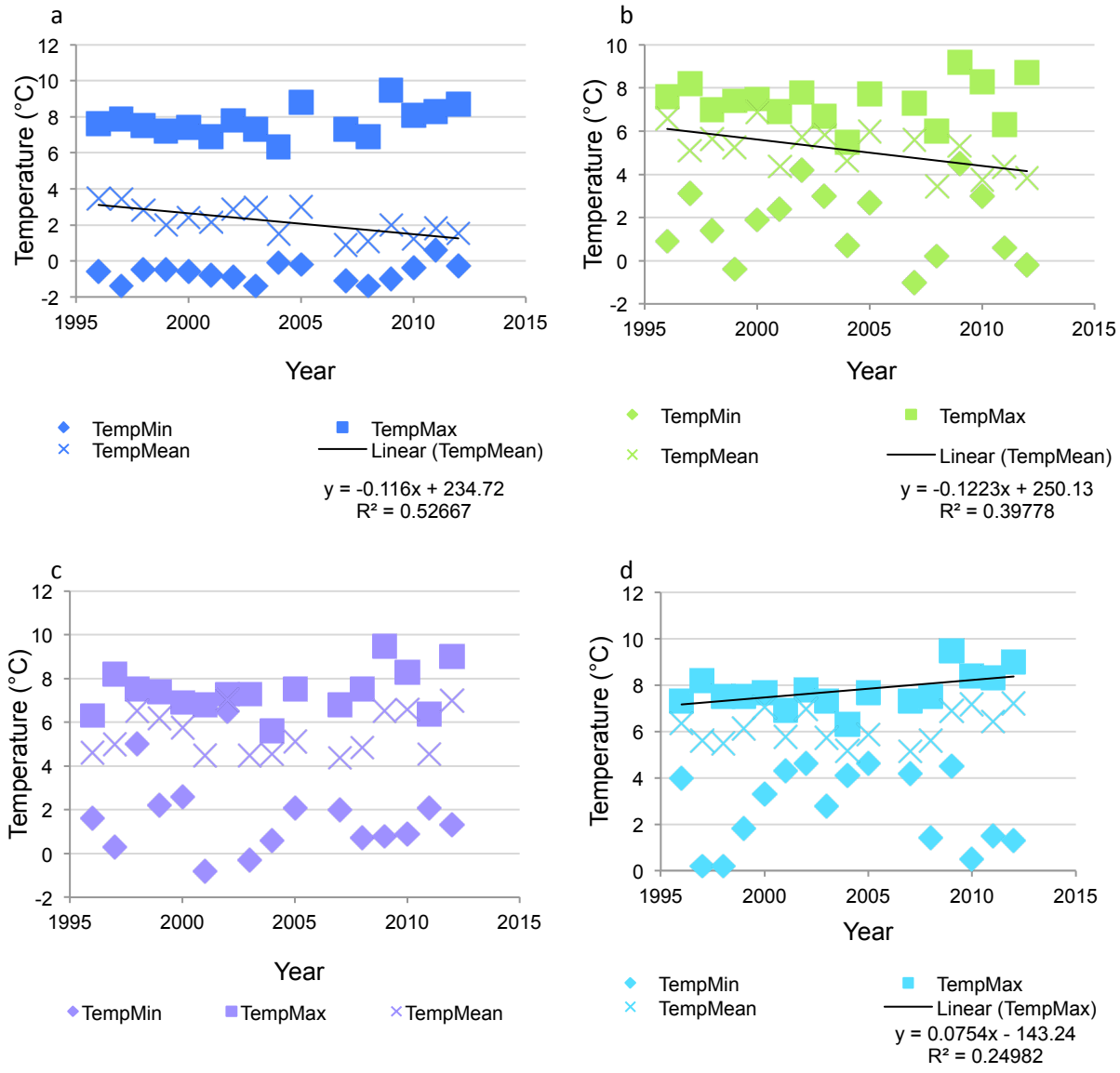

Figure 2.10a-d: Minimum and maximum temperature of occurrence and mean temperature of abundance using DFO data from 1996-2012. Trend lines were calculated from linear regression models with time as the explanatory variable. a: Atlantic cod, mean temperature of cod abundance decreased significantly over time ($p < 0.05$); b: haddock, mean temperature of haddock abundance decreased significantly over time ($p < 0.05$); c: pollock, no significant temperature changes ($p > 0.18$); and d: silver hake, maximum temperature of silver hake occurrence increased significantly over time ($p < 0.05$).

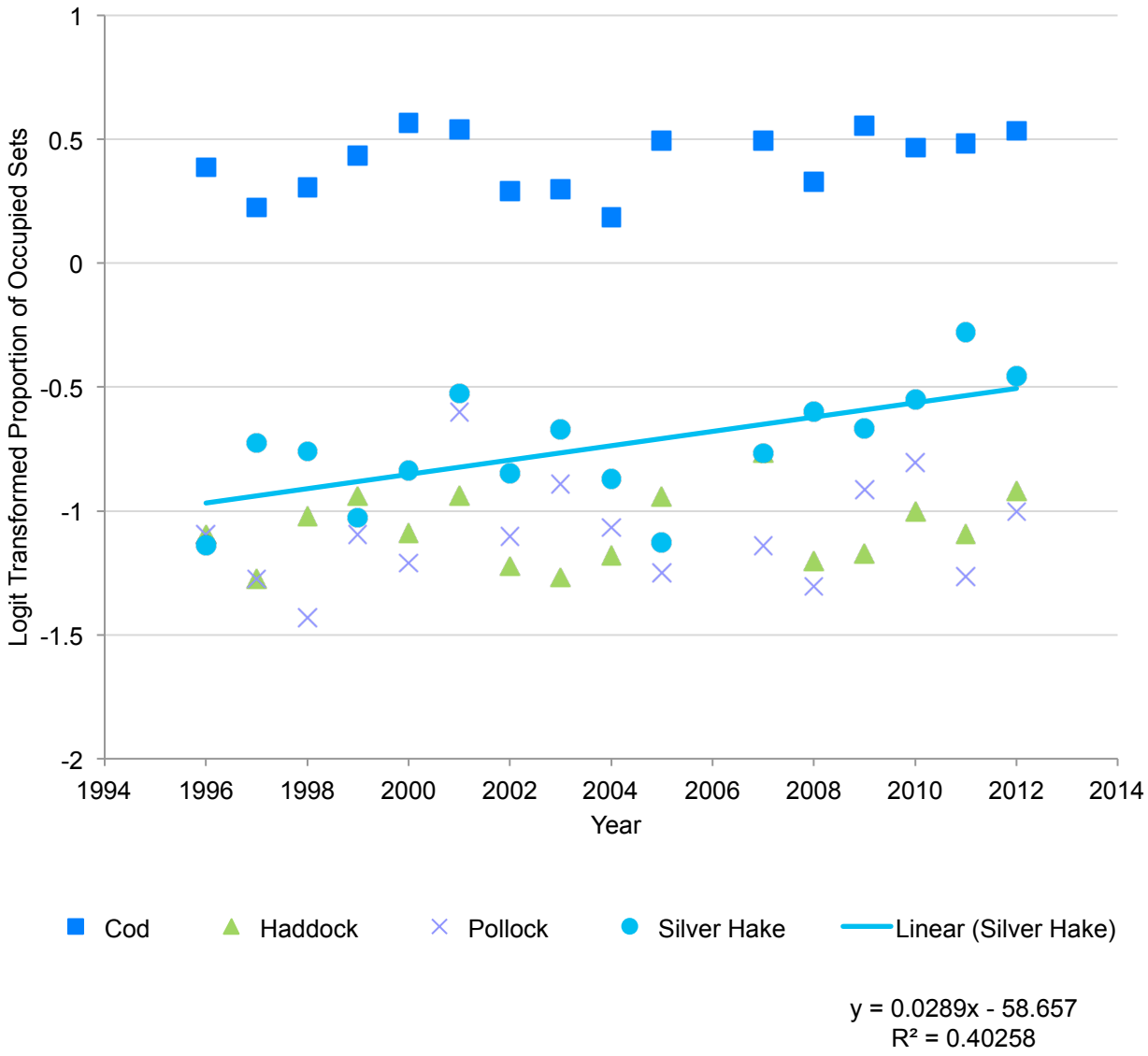

Figure 2.11: The logit-transformed percentage of occupied sets for four gadoid species over 16 years to illustrate range expansions and contractions. The trend line was calculated from a linear regression model with time as the explanatory variable. Silver hake exhibited a significant increase ($p < 0.01$).

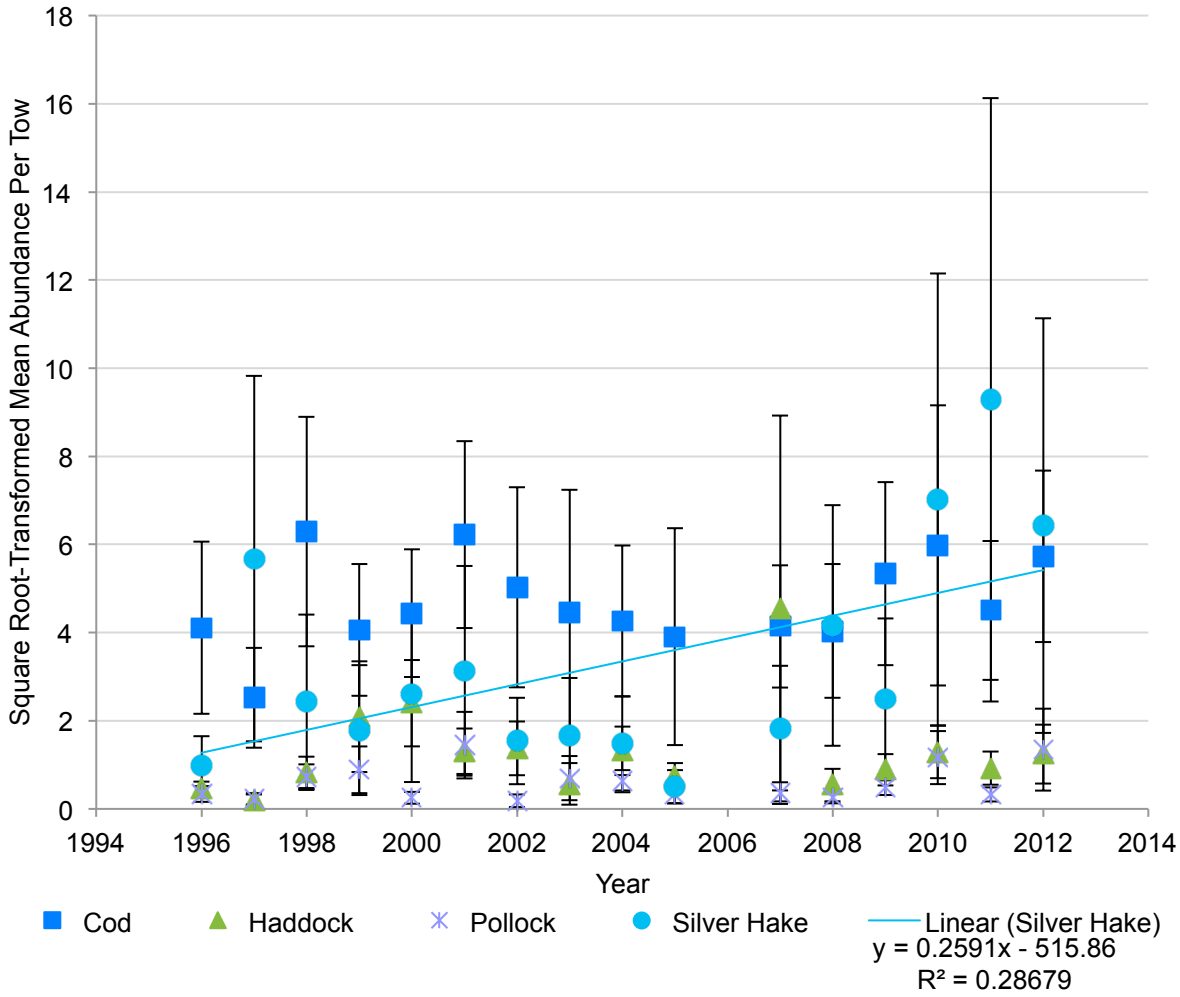

Figure 2.12: The square root-transformed, design-weighted mean number per tow of four gadoid species over 16 years to illustrate changes in abundances. The trend line was calculated from a linear regression model with time as the explanatory variable. Silver hake exhibited a significant increase ($p < 0.05$).

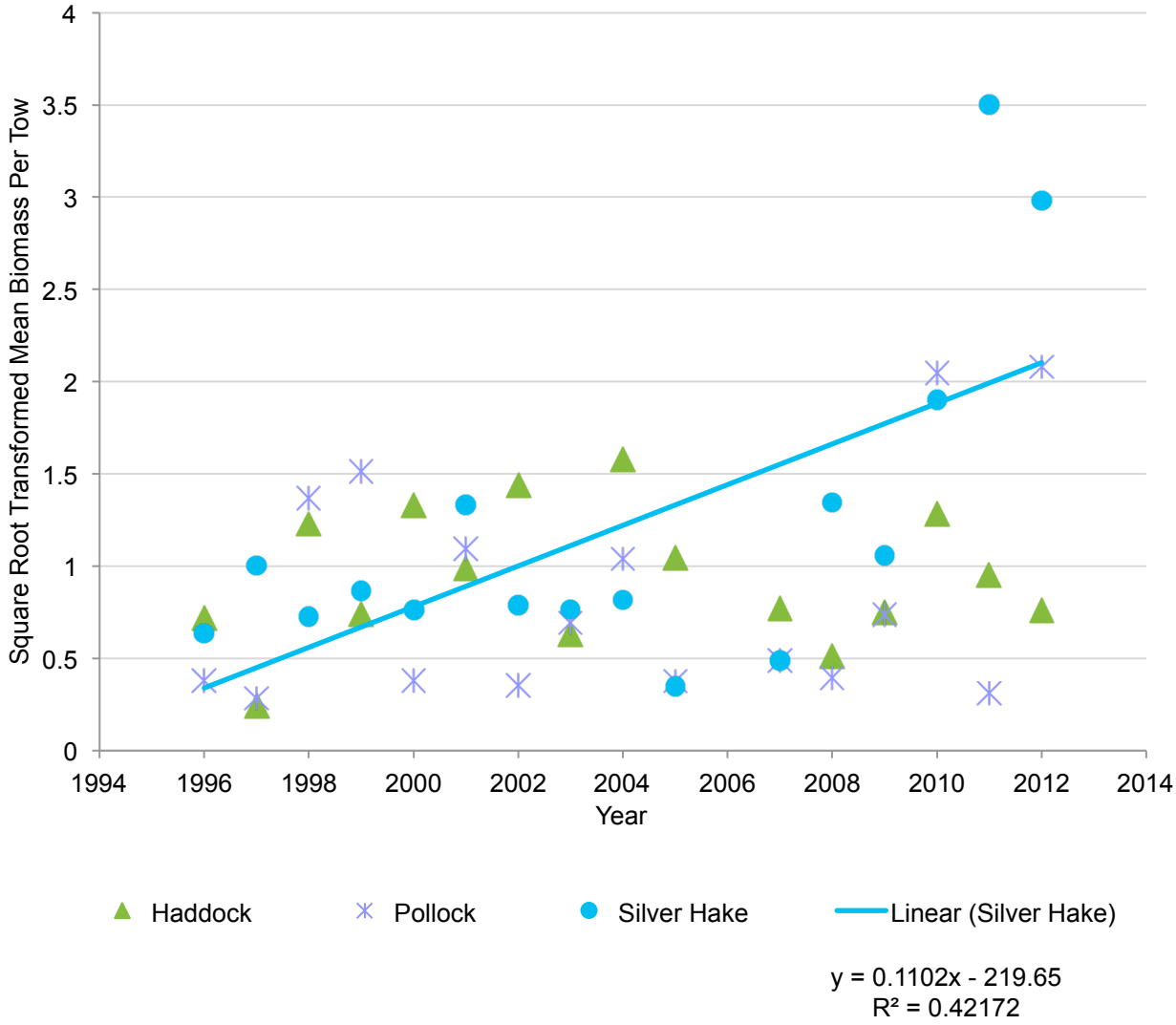

Figure 2.13: The square root-transformed, design-weighted mean biomass per tow per year of three non-cod gadoids over 16 years using DFO data from 1996-2012. The trend line was calculated from a linear regression model with time as the explanatory variable. Silver hake exhibited a significant increase ($p < 0.05$).

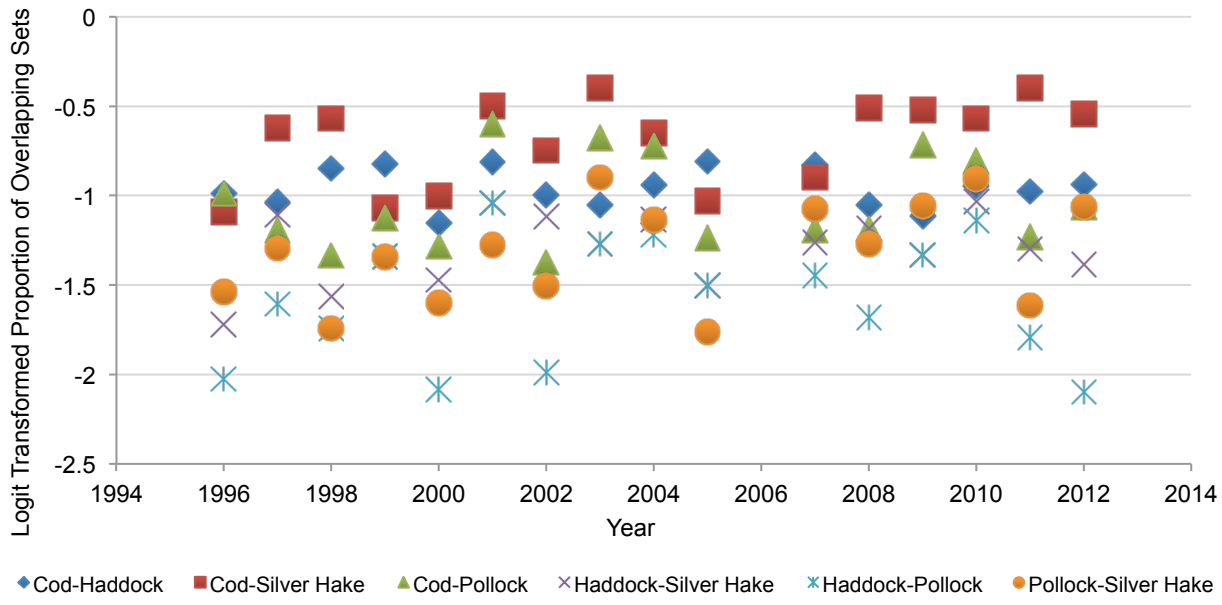

Figure 2.14: The logit-transformed proportions of co-occurring sets for six species pairs over time. No statistically significant changes in overlap were measured over time.

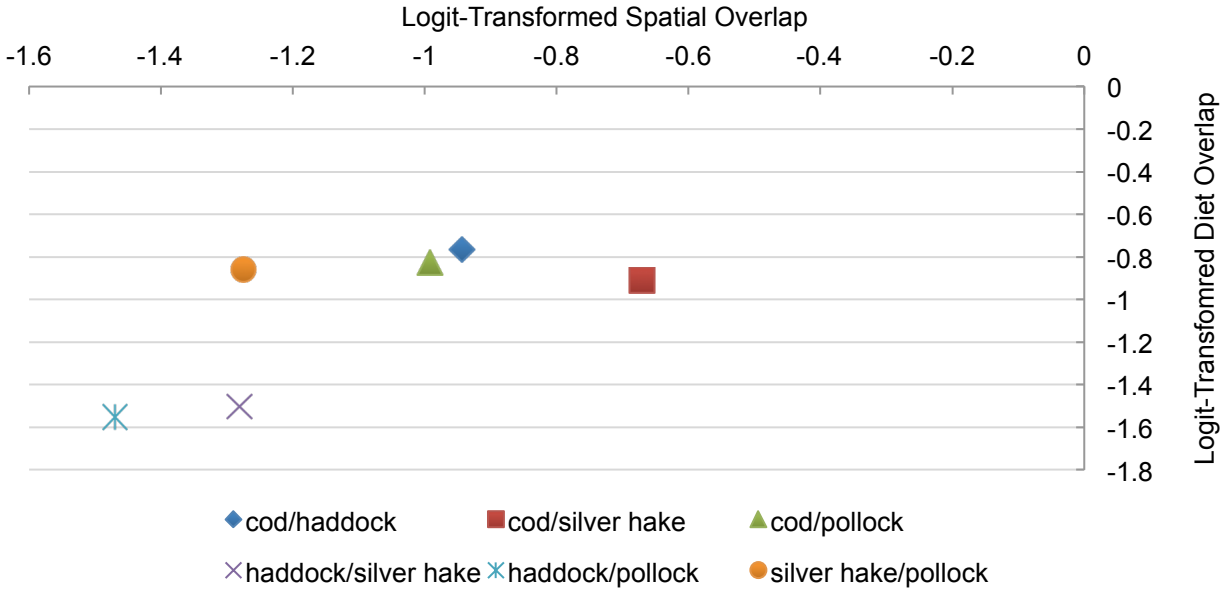

Figure 2.15: Pairwise comparisons of the logit-transformed degree of spatial and diet overlap of four gadoid species. There was a statistically significant positive relationship between the two ($p < 0.05$).

General Conclusion

This study quantified, provided evidence for, and brought forward statistically significant biogeographical correlations and potential shifts that corresponded to changes in ocean conditions, specifically increases in bottom temperatures in southern Newfoundland waters. As ecosystem level processes are exceedingly complex and often the result of multiple, synergistic stressors (Doney et al. 2012), we were only able to conclude that warming was one driver of change in this ecosystem, and it was certainly associated with observed, quantified biotic changes. As mentioned previously, these results can be relevant to stock assessments and ecosystem-based fisheries management (Link 2002a, Link et al. 2011), as well as researching the overall structure and productivity of marine ecosystems (Walters et al. 1999, Walther et al. 2002).

Kempf et al. (2010) highlighted the importance of including competitive and predatory interactions into an ecosystem approach to fisheries management, as the assumption of constant natural mortality can lead to impractical and inaccurate forecasts. This is especially relevant in ecosystems experiencing an emergence of species that are known to prey upon the early life history stages of a commercially targeted species, which can affect stock rebuilding. In these cases, studying the extent of these species' increases and composition of their diets can lead to more accurate stock assessment models and fisheries management advice (Ulltang 1996, Link 2002b).

The aforementioned conditions accurately describe my study area NAFO Subdivision 3Ps, which is considered a thermal transition zone and contains the northern range endpoints of some gadoid species (Pinhorn and Halliday 1997). Measured increases in bottom temperatures in

this region since the early 1990s were expected to initiate responses in the ecosystem particularly related to changes in spatial distributions (Drinkwater 2005, Rose 2005a) and altered trophic interactions (Walther et al. 2002, Winder and Schindler 2004). The goals of my research were to first investigate whether statistically significant warming that has been observed and measured over the past two decades corresponded with changes of four gadoid species in the ecosystem, and to quantify such changes. These included diet composition, interspecific competition, and intraguild predation, as well as shifts in spatial distribution and extent, abundance, and biomass. This study also sought to examine the connection between diet and spatial overlap if it was found to exist in 3Ps.

This study dealt with a number of hypotheses related to diet and spatial distribution. For the diet aspect of my study, many of the comparisons were with stocks in adjacent ecosystems, as diets of non-cod gadoids in this region represent a knowledge gap. The hypotheses associated with the spatial portion of my research were that in response to warming, there would be increases in mean latitude of abundance, changes in mean depth and temperature of abundance; spatial range expansions of warmer water species and/or contractions of resident, cooler water species; and changes in biomass, abundance, or both. It was also hypothesized that latitude would be a less informative metric for measuring spatial shifts due to differences in thermal thresholds of the study species, and potential exclusion of these species along the latitudinal gradient.

Compared to adjacent, more southerly ecosystems, I found that silver hake were consuming more invertebrates, and less finfish prey, although this may be the result of the narrow size range of fish that were sampled, as piscivory appeared to increase with increasing length. Overall, pollock was the most piscivorous species, but catches on both the CFER and

DFO surveys were patchy, and the diet data came from relatively few fishing sets over the course of two years. Pollock had the smallest observed abundances of all four species. Haddock diet was predominantly comprised of benthic organisms, and this species had the most intraspecifically consistent diet of the gadoids sampled. However, most stomach samples from this species were from the eastern edge of 3Ps, and the majority of samples collected in 2014 were technically from 3O, meaning the haddock stomachs that were sampled were unlikely to have co-occurred with the other species that were sampled. Atlantic cod was the most thoroughly sampled species, and had the least consistent diet. Cod is known to be an opportunistic generalist (Link and Almeida 2000); therefore this result is consistent with other studies. However, in ecosystems farther south, and even within 3Ps in previous decades, cod diet consisted of more finfish prey (Cook and Bundy 2010). In this study, cod was found to prey heavily upon snow crab and other crab species, especially in 2013, and only consumed significant quantities of sandlance in 2014. This may be indicative of an ecosystem in transition, if cod are switching from energy rich finfish prey to less desirable crustacean species. Continued study of gadoid food habits is recommended to track the progression of this observation. DFO is now expanding stomach content sampling in Newfoundland waters to include silver hake.

When quantifying species interactions through interspecific diet overlap and competition, it was found that all diets were functionally different and there was no evidence of intraguild predation on the shelf edges, slopes, and channels in 3Ps where and when we sampled in the spring. Therefore, it can be concluded that competition and predation in 3Ps at this time of year was low. This may be the result of low levels of spatial overlap. Even within the same location, the species were often stratified by depth, with Atlantic cod inhabiting the shallowest waters, silver hake in the deepest, and haddock and pollock at intermediate depths. This would mean that

the four species were accessing different prey species in different areas of the water column, and not encountering one another as potential prey, even within the same area (Mullowney et al. 2012). Therefore it is unlikely that single species dynamics are being driven by interactions with the other species of interest.

In the study of gadoid spatial distributions in southern Newfoundland waters over the past 17 years, the most notable shifts were seen in silver hake that exhibited statistically significant increases in maximum temperature of occurrence, mean latitude of abundance, areal extent, and overall biomass and abundance between 1996 and 2012. It is notable that these changes occurred outside of the stock management area and the data for this stock, or portion of the stock, have not been incorporated into assessment advice for the adjacent Scotian Shelf stock (Stone et al. 2013). The results found here support the need for continued and more in depth research of silver hake in southern Newfoundland waters.

The mean latitude of pollock abundance increased by an average of 0.042°N, or about 4.5 kilometers per year over the time series, but no other statistically significant spatial changes were observed. Haddock decreased its mean temperature of abundance, along with cod. Atlantic cod also had an observed decrease in mean depth of abundance, but at a rate that was unprecedented. Using methods from Dulvy et al. (2008) and Nye et al. (2009), it was calculated that cod abundance moved into shallower waters at an average rate of 4.815 meters per year over the time series. In Dulvy et al. (2008), species' ranges were found to deepen at a rate within the range of 0.6 to 1.4 meters per decade. The reasons for such a rapid ascent in abundance are not fully understood, and emphasize the uniqueness of 3Ps and its fish stocks.

However, it should be noted that this was a measured shift of abundance, and not biomass, which was one limitation that arose from using size- and age-aggregated abundance data. Without details concerning age or size composition of the set, we were not able to conclude definitively whether changes in cod distribution were the result of an overall shift to cooler, shallower waters, or a fishing effect. While younger and smaller fish inhabit shallow shelf habitat, larger, more mature fish are found at warmer temperatures and in deeper channels (Kao and Fletcher 1988). Catching larger quantities of younger, smaller cod in the survey could result from the fishery removing the majority of the large cod from the population. Therefore, an analysis of the biomass and the size and age structure of these sets should be considered.

Aside from fishing mortality, two other hypotheses include episodic recruitment and poor survival of larger, older fish from other biotic and abiotic stressors, both of which are supported by DFO research (DFO 2014a, DFO 2015a). Extraordinarily large year classes of Atlantic cod in 2011 and 2012 (DFO 2015a) support the recruitment theory, and in recent years total mortality rates, which include mortality due to fishing and all other causes, of cod aged 5-10 have been much higher than the time series average (DFO 2015a). Because less than half of the total allowable catch has been reported as landed, these rates may be indicative of some other cause of mortality. The age range for which these rates are calculated could support the hypothesis of poor survival of older year classes, leading to an increase in the quantity of younger fish being collected in the survey, while overall abundance remains around the time series average (DFO 2015a). Analysis of the DFO survey catch biomass data over time would give a more inclusive view of the size and age structure of the survey catch, and by extension, the stock. These data would help support or reject the possibility of an environmental or exploitation effect. With this

information, we could determine more conclusively whether the cod population is exhibiting an overall shift into shallower waters.

CFER has adopted an approach to ecosystem monitoring and research targeted at specific research questions. This ecosystem-based approach seeks to compliment and improve traditional single-species methods. To accomplish this objective, CFER has expanded its sampling protocols to include not only cod, but other species found in southern Newfoundland. It is through this ecosystem approach that my research was developed, with a goal to achieve a broader look at the populations in this ecosystem to maximize both ecological understanding and future commercial potential for established as well as emerging stocks. My work with stomach content analysis and spatial distributions may help future researchers create more accurate food web models and better understand the stocks in relation to trophic interactions and their distributions and abundances. These data will increase understanding of the impacts of changes in biogeography and population structure thought to be driven by changing ocean conditions, and the resultant impacts on the fishing industry of Newfoundland and Labrador. Finally, the present study was proposed in order to quantify data that were largely anecdotal. Harvesters and researchers were coming across southern species, especially silver hake, more frequently. Now that it has been shown that there is a significant shift occurring in this ecosystem, more specific questions related to the origin, extent, and residence of southern species can be investigated.

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Appendix: Set and catch details from the CFER surveys spring 2012-2014.

Table A.1: Fishing set date, time, duration, location, depth, and bottom temperature from the CFER surveys.

Set Number	Date	Start Time	Duration (min)	Latitude	Longitude	Depth (m)	Temperature (◦C)
1205	12/5/12	1119	17	46.997	-56.084	167	-0.1
1206	12/5/12	1730	15	47.393	-55.566	230	1.9
1207	12/5/12	2214	18	47.494	-55.173	200	1.7
1208	13/5/12	0738	15	47.508	-56.31	272	7.1
1209	13/5/12	1915	15	47.4	-57.817	225	6.6
1210	14/5/12	1332	15	47.218	-57.384	183	5.5
1211	14/5/12	1903	12	47.13	-58.215	242	7.8
1212	14/5/12	2149	15	47.134	-57.782	72	2.2
1213	14/5/12	2322	15	47.135	-57.671	105	1.7
1214	15/5/12	0904	11	47.007	-58.049	123	2.8
1215	16/5/12	1341	15	46.882	-57.102	180	6.6
1216	18/5/12	1038	15	45.84	-56.81	194	8.7
1217	19/5/12	0008	15	45.311	-56.366	218	7.3
1218	19/5/12	1409	15	44.999	-55.682	104	5.7
1219	20/5/12	0840	15	45.18	-55.333	160	8.3
1220	20/5/12	1013	20	45.156	-55.499	145	7.7
1221	20/5/12	1256	21	45.184	-55.021	145	7.9
1222	20/5/12	1902	15	45.231	-55.019	143	7.9
1223	20/5/12	2026	16	45.256	-55.13	173	8
1224	21/5/12	1201	16	45.417	-55.178	142	1
1225	21/5/12	1858	16	45.505	-55.145	124	0.5
1226	21/5/12	2041	16	45.517	-55.261	148	0.9
1227	21/5/12	2346	15	45.58	-55.252	156	1
1228	22/5/12	0922	16	45.834	-54.886	71	0.1
1229	22/5/12	1524	17	45.919	-55.132	165	0.1
1230	22/5/12	2219	22	46.086	-55.256	136	0.1
1352	16/5/13	1942	16	45.332	-55.691	89	0.4

Set Number	Date	Start Time	Duration (min)	Latitude	Longitude	Depth (m)	Temperature (◦C)
1353	16/5/13	2238	16	45.394	-55.033	129	4.3
1354	17/5/13	1041	6	45.249	-55.393	161	7.6
1355	17/5/13	1348	6	45.167	-55.636	97	0.4
1356	17/5/13	1538	15	45.168	-55.472	145	7.2
1357	18/5/13	0944	15	45.082	-55.38	145	7.2
1358	18/5/13	1256	15	45.131	-54.979	130	0.6
1407	26/4/14	1855	6	45.186	-54.33	106	1.6
1408	27/4/14	0018	7	45.0634	-54.6574	229	8.2
1409	27/4/14	1146	6	45.3695	-55.2231	158	7.8
1410	27/4/14	1539	6	45.097	-55.44	179	7.4
1411	27/4/14	2131	6	44.9051	-55.7471	244	7.3
1412	28/4/14	1045	16	45.1861	-54.3304	108	0.9
1413	29/4/14	1056	6	45.9517	-56.9432	248	7.8
1414	29/4/14	1634	6	46.357	-57.276	129	1.1
1415	29/4/14	1846	6	46.4104	-57.3189	81	1.4
1416	29/4/14	2151	7	46.45	-57.504	346	6
1417	30/4/14	1053	6	45.5803	-56.5234	103	1
1418	30/4/14	1221	5	45.6112	-56.569	157	3
1419	30/4/14	1520	5	45.6485	-56.627	213	7.5
1420	30/4/14	1732	5	45.6861	-56.693	257	8.1
1421	1/5/14	0048	5	44.9284	-56.0808	152	7
1422	1/5/14	1112	6	45.0207	-56.051	104	1
1423	1/5/14	1323	6	44.933	-55.7714	153	3.2
1424	1/5/14	1600	6	45.0299	-55.7002	95	0.4
1425	1/5/14	1835	6	45.0757	-55.6132	105	0.4
1426	1/5/14	2141	5	45.0116	-55.2648	206	8.3
1427	1/5/14	2303	6	45.0288	-55.3892	192	7.6
1428	2/5/14	1116	6	45.0817	-54.4906	221	6.7
1429	2/5/14	1300	6	45.0655	-54.487	259	7
1430	2/5/14	1430	6	45.0859	-54.4592	177	2.9
1431	2/5/14	1654	6	45.2068	-54.2437	92	-0.6
1432	2/5/14	2030	6	45.1327	-54.3702	128	5.6

Table A.2: Catches of four species in all sets (2012-2014) from the CFER surveys (in order of increasing bottom temperature) N_C: number of fish caught, N_A: number of stomach samples used in statistical analyses for Chapter 1.

			Cod		Haddock		Pollock		Silver Hake	
Year Set	Depth (m)	Temp (◦C)	Weight (kg)	N_C/N_A	Weight (kg)	N_C/N_A	Weight (kg)	N_C/N_A	Weight (kg)	N_C/N_A
1431	92	-0.6	2.18	11/0	0	0	0	0	0	0
1205	167	-0.1	100.77	205/100	0	0	0	0	0	0
1228	71	0.1	15.43	41/34	0	0	0	0	0	0
1229	165	0.1	32.2	43/39	0	0	0	0	0	0
1230	136	0.1	12.45	16/14	0	0	0	0	0	0
1352	89	0.4	20	37/34	0	0	0	0	0	0
1355	97	0.4	28.8	137/137	0	0	0	0	0	0
1424	95	0.4	1.52	5/4	0	0	0	0	0.12	1/0
1425	105	0.4	51.72	150/146	0	0	0	0	0	0
1225	124	0.5	143.24	147/68	0	0	0	0	0	0
1358	130	0.6	114.1	87/72	86.05	77/0	55.7	25/25	0.3	1/0
1226	148	0.9	132.96	109/0	3.71	1/0	0	0	0	0
1412	108	0.9	22.04	15/11	494.22	432/43	25.96	10/9	20.06	57/28
1224	142	1	49.89	41/40	372.84	218/62	0	0	0	0
1227	156	1	8.71	9/9	0	0	0	0	0	0
1417	103	1	0.144	14/0	0	0	0	0	0	0
1422	104	1	1.18	17/16	0	0	0	0	0	0
1414	129	1.1	1.96	1/0	0	0	0	0	0.16	1/1
1415	81	1.4	1.52	12/7	0	0	0	0	0	0
1407	106	1.6	6.2	6/5	218.5	183/43	68.64	26/26	1.24	4/3
1207	200	1.7	60.19	67/61	0	0	0	0	0	0
1213	105	1.7	24.27	62/53	0	0	0	0	0	0
1206	230	1.9	81.19	125/116	0	0	0	0	0	0
1212	72	2.2	13.63	24/22	0	0	0	0	0	0
1214	123	2.8	109.46	235/115	0	0	0.66	1/0	0	0

			Cod		Haddock		Pollock		Silver Hake	
Year Set	Depth (m)	Temp (◦C)	Weight (kg)	N_C/N_A	Weight (kg)	N_C/N_A	Weight (kg)	N_C/N_A	Weight (kg)	N_C/N_A
1430	177	2.9	0	0	0	0	0	0	10.9	42/14
1418	157	3	1.12	1/0	0	0	0	0	70.6	808/23
1423	153	3.2	0	0	0	0	0	0	49.46	230/28
1353	129	4.3	166.64	174/142	144.1	149/144	0	0	0	0
1210	183	5.5	10.23	12/12	0	0	1.25	2/0	0	0
1432	128	5.6	0	0	19.72	21/21	6	2/2	20.88	62/28
1218	104	5.7	432.05	775/145	0.54	1/0	0	0	0.1	1/0
1416	346	6	0	0	0	0	0	0	12.77	16/5
1209	225	6.6	1.07	2/1	0	0	0	0	0.47	5/0
1215	180	6.6	9.67	17/10	25.94	32/29	0	0	2.81	11/0
1428	221	6.7	34.42	8/2	0	0	0	0	3.6	12/7
1421	152	7	0	0	3.32	5/0	572.14	355/44	14.36	93/19
1429	259	7	0	0	0	0	0	0	2.24	11/2
1208	272	7.1	3.86	8/6	0	0	0	0	0	0
1356	145	7.2	74.67	36/22	324.02	950/0	116.4	57/0	0	0
1357	145	7.2	3.49	3/3	61.83	204/0	672.08	491/87	0.68	4/0
1217	218	7.3	0	0	0	0	0	0	24.77	113/0
1411	244	7.3	1.59	1/0	0	0	0	0	85.1	480/15
1410	179	7.4	9.94	5/5	0	0	2.75	1/1	2.1	9/6
1419	213	7.5	0	0	0	0	0	0	186.69	1394/30
1354	161	7.6	0	0	2.7	21/21	0	0	9.1	31/27
1427	192	7.6	0	0	1.93	3/3	0	0	31.02	144/26
1220	145	7.7	55.63	48/44	22.25	25/25	0	0	0	0
1211	242	7.8	2.6	4/3	0	0	0	0	6.68	26/0
1409	158	7.8	63.88	15/8	1.62	4/4	3	1/1	10.78	42/20
1413	248	7.8	3.26	1/1	4.74	2/2	2.38	1/1	63.86	442/41
1221	145	7.9	0.01	1/0	8.33	17/12	0	0	18.87	60/12
1222	143	7.9	12.56	10/7	4.09	5/3	0	0	5.53	12/8
1223	173	8	0.64	1/1	49.31	37/27	0	0	2.16	7/1
1420	257	8.1	0.38	1/0	0	0	0	0	226.24	1414/23

			Cod		Haddock		Pollock		Silver Hake	
Year Set	Depth (m)	Temp (◦C)	Weight (kg)	N_C/N_A	Weight (kg)	N_C/N_A	Weight (kg)	N_C/N_A	Weight (kg)	N_C/N_A
1408	229	8.2	0	0	0	0	0	0	59.14	364/15
1219	160	8.3	1.75	1/0	1.99	12/4	0	0	13.94	41/37
1426	206	8.3	2.4	5/5	0.55	1/1	0	0	5.38	15/7
1216	194	8.7	1.31	2/2	6.81	4/4	0	0	40.67	218/0

Table A.3: Number of empty stomachs by species caught in CFER surveys.

Species	# of Stomach Samples	# With Contents	# Empty	Percentage Empty
Atlantic Cod	1681	1522	159	9.46
Haddock	476	448	28	5.88
Pollock	212	196	16	7.55
Silver Hake	588	419	169	28.74

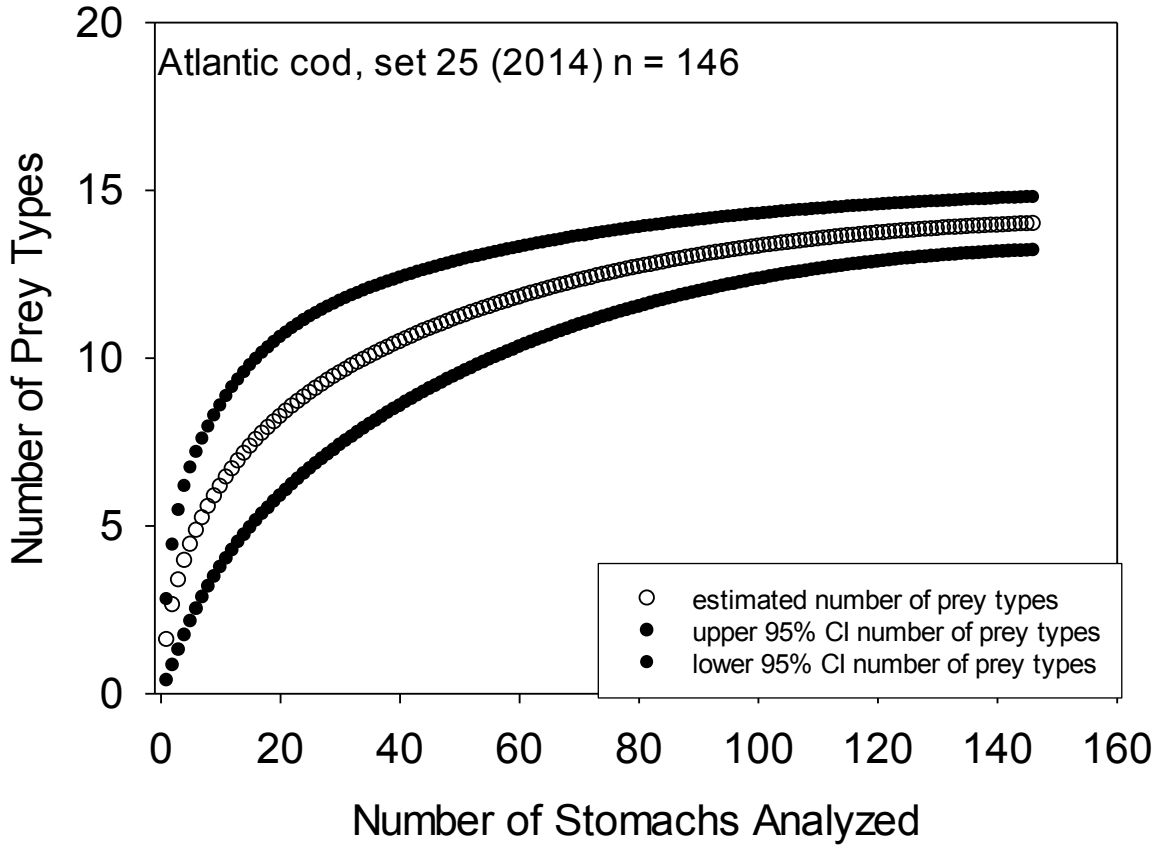

Figure A.1a: Randomized prey accumulation curves with 95% confidence intervals generated using *EstimateS* software (Colwell 2013) for Atlantic cod. This set was illustrated because it was the largest collection of stomachs within a set for this species within the years 2012-2014.

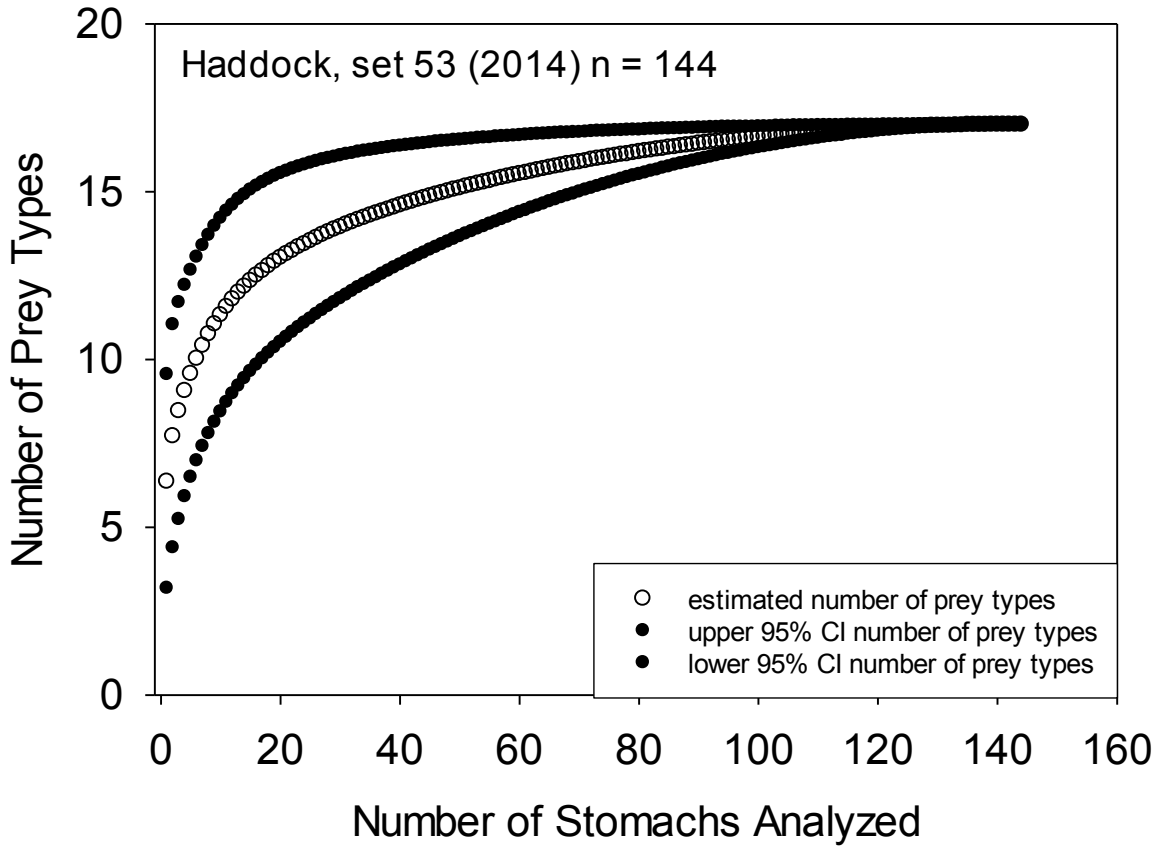

Figure A.1b: Randomized prey accumulation curves with 95% confidence intervals generated using *EstimateS* software (Colwell 2013) for haddock. This set was illustrated because it was the largest collection of stomachs within a set for this species within the years 2012-2014.

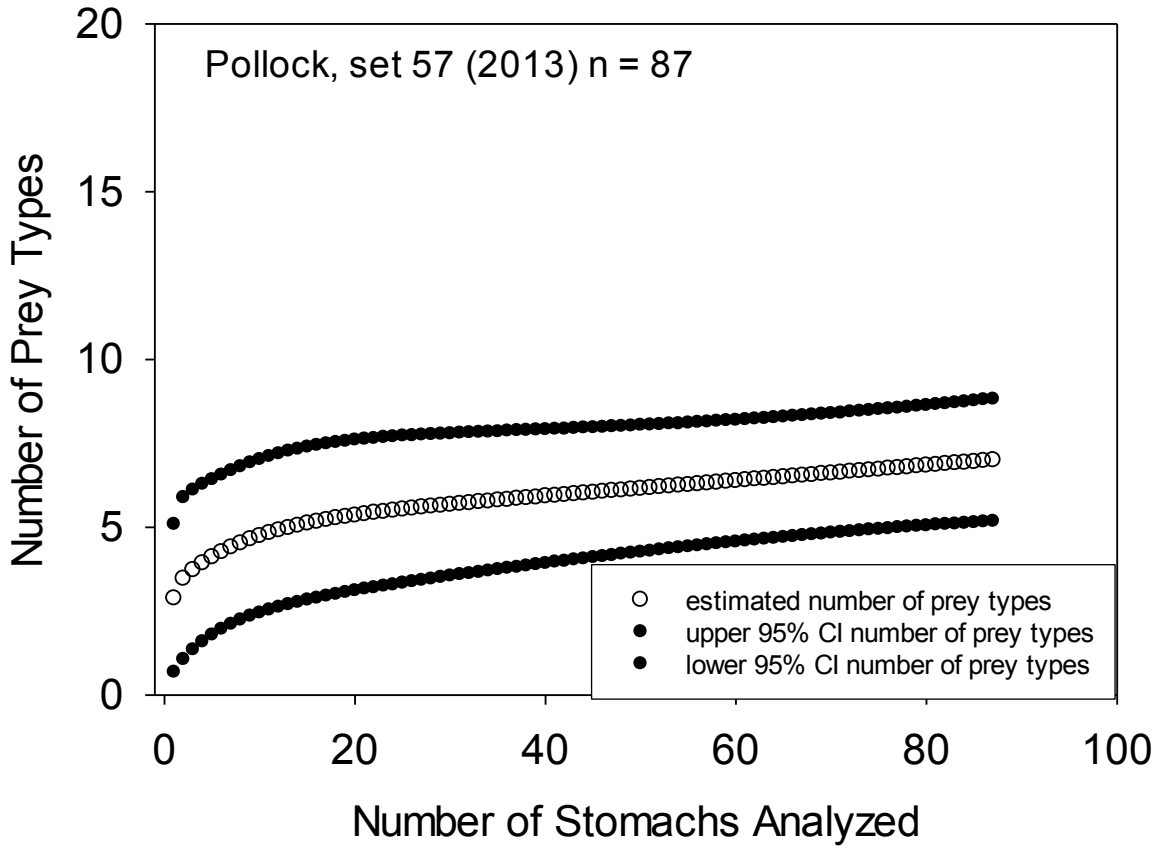

Figure A.1c: Randomized prey accumulation curves with 95% confidence intervals generated using *EstimateS* software (Colwell 2013) for pollock. This set was illustrated because it was the largest collection of stomachs within a set for this species within the years 2012-2014.

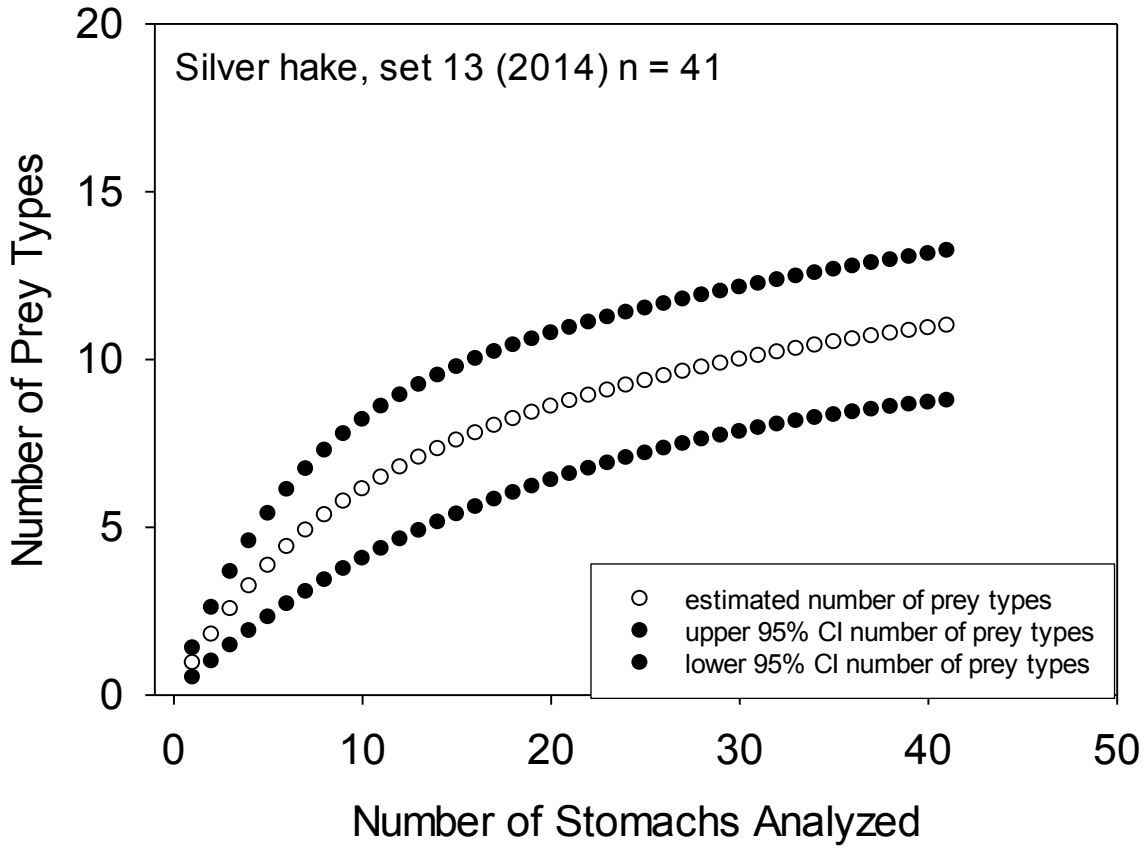

Figure A.1d: Randomized prey accumulation curves with 95% confidence intervals generated using *EstimateS* software (Colwell 2013) for silver hake. This set was illustrated because it was the largest collection of stomachs within a set for this species within the years 2012-2014.

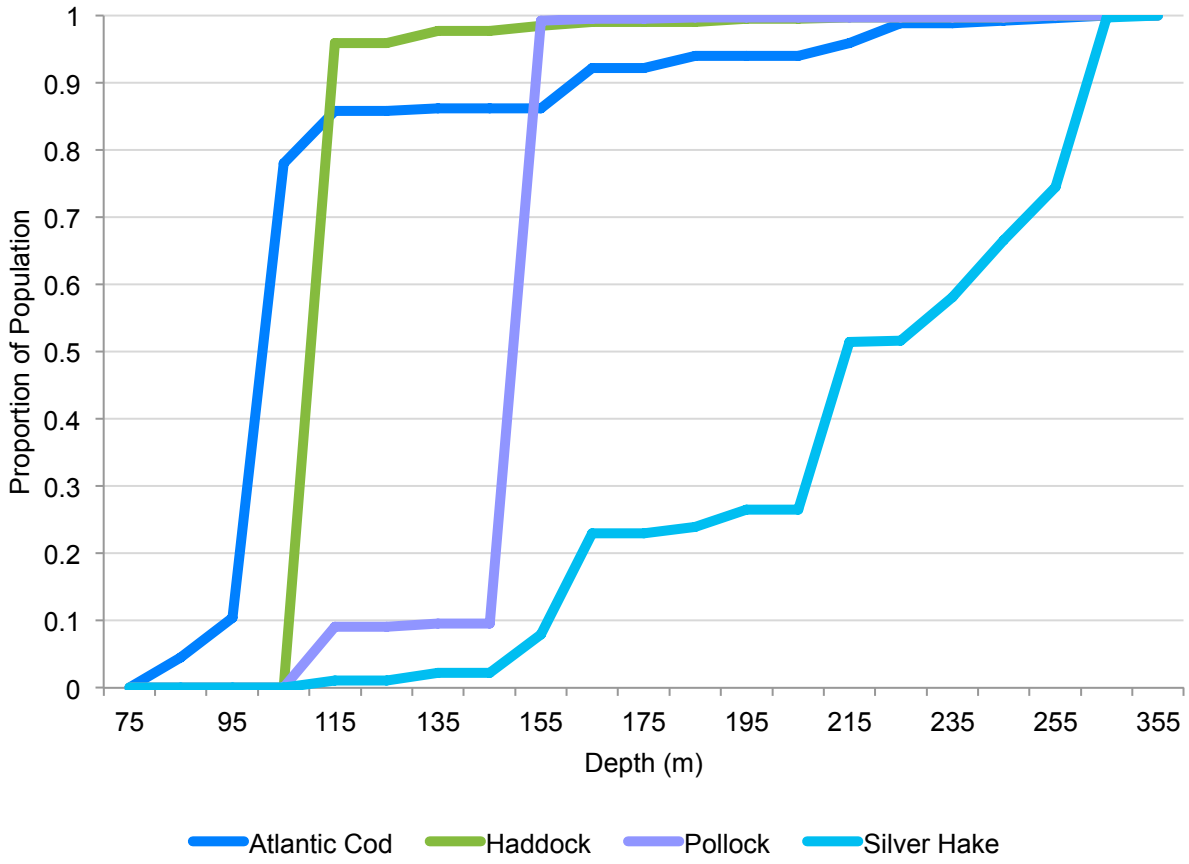

Figure A.2: Cumulative distribution of species caught by depth from the 2014 CFER survey.

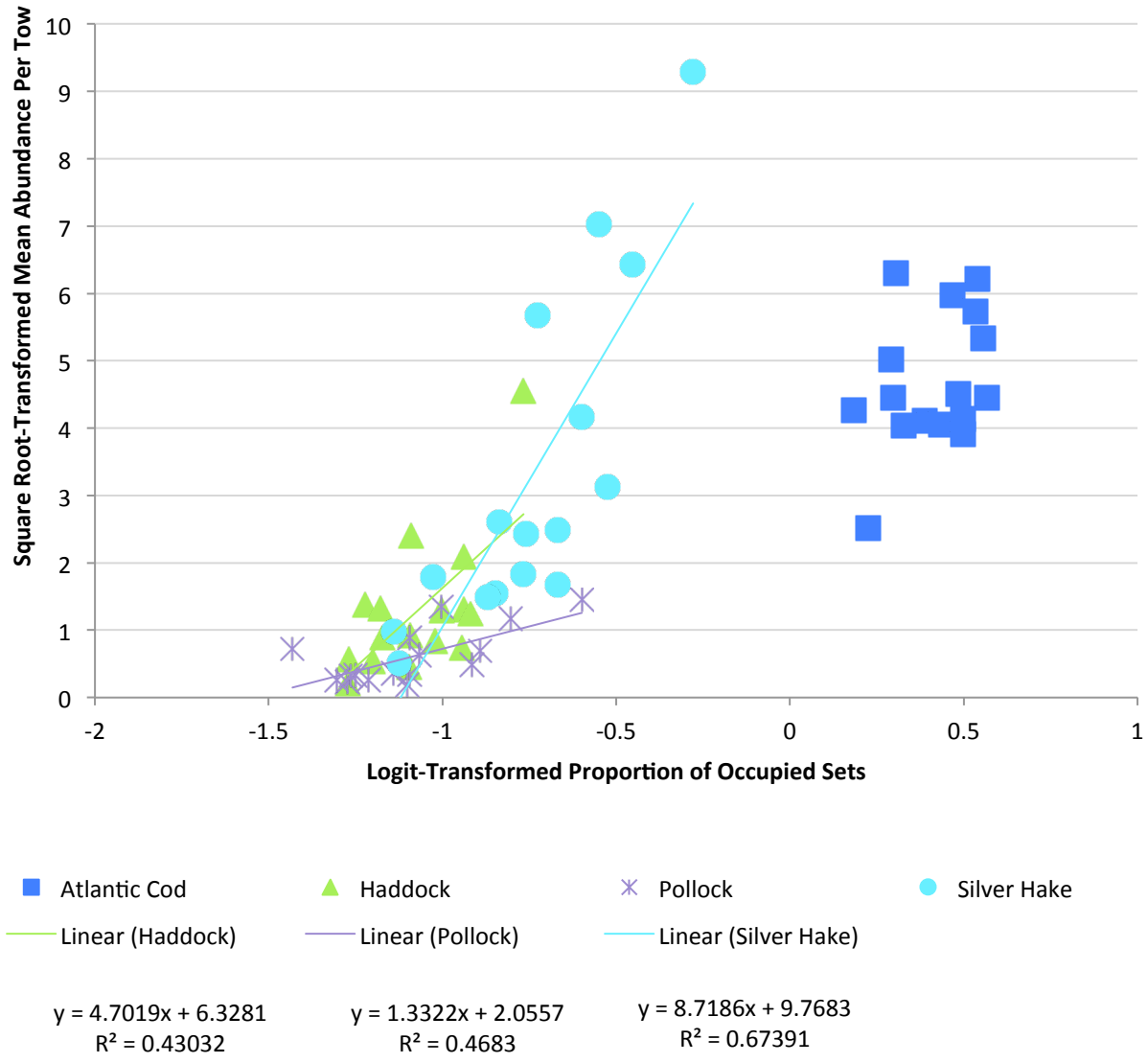

Figure A.3: The relationship between spatial distribution and design-weighted abundance. There was a significant positive relationship for three non-cod gadoid species.